



Global dynamics of a diffusive competition model with habitat degradation

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Abstract

In this paper, we propose a diffusive competition model with habitat degradation and homogeneous Neumann boundary conditions in a bounded domain that is partitioned into the healthy region (undisturbed habitat) and the degraded region (due to anthropogenic habitat disturbance). Species follow the Lotka-Volterra competition in the healthy region while in the degraded region species experience only exponential decay (not necessarily at the same rate). This setup is novel in that it requires no positivity assumption on the environmental heterogeneity, either absolute or on average, which would be far too restrictive for the study of the effects of habitat degradation. We rigorously show competitive exclusion and coexistence via global stability analysis. A remarkable finding is that the quality heterogeneity of landscapes can lead to the competitive exclusion of the slower species by the faster species. This result is robust as long as the degraded region has positive area, and moreover is at odds with classical results predicting the deterministic extinction of the stronger species. On the other hand, if the degraded region has intermediate negative effect on the faster competitor, species can coexist. Differing from comparable existing results, coexistence does not rely on a limit as the diffusion coefficients tend to zero or infinity. Together, these results imply that coexistence is always a possibility under this basic, yet general, configuration, providing insights into the varying impacts found through empirical study of habitat loss and fragmentation on species.

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1 Introduction

1.1 Motivation

Habitat loss, caused by anthropogenic activities or natural processes, has drastic negative effects on virtually all species worldwide (Heinrichsa et al. 2016), particularly on population persistence and biodiversity. This includes birds (Temple 1986), mammals (Andren 1994), reptiles (Gibbons et al. 2000), amphibians (Stuart et al. 2004; Beebee and Griffiths 2005), invertebrates (Didham et al. 1996), and plants (Hobbs and Yates 2003). Habitat loss has been one main culprit of species extinction worldwide, see (Pimm and Raven 2000) and more recently (Betts and et al. 2019). Causes of habitat loss can be naturally driven, such as forest fires, volcanic activity, hurricanes etc., but can also be driven by human activities, such as land conversion for the use of farming, harvesting natural resources, urban sprawl, or infrastructure development. However, even indirect actions can lead to the collapse of habitat, such as desertification, deforestation, pollution, or a continual degradation of the habitat to a point where it can no longer support its native species.

The extinction of species has been a serious concern in conservation biology and can result in additional negative impacts, such as a reduction of genetic diversity within a species. For example, 67% of North American freshwater mussel species are considered threatened, and 35 species have gone extinct since 1900 (Nobles and Zhang 2011). Mussels filter lake/river water for their own food and are consumed by a wide variety of carnivores at higher trophic levels, such as otters and egrets. These intimate and sophisticated connections between interacting species, paired with the delicate balance in an ecosystem, provide substantial motivation for studying habitat degradation and destruction and its effects on biodiversity and sustainability of an ecosystem. In this example, habitat loss has been one of the major contributors to the decline and extinction of freshwater mussels.

It is unfortunate, therefore, that despite our receptivity to the ideas presented by biologists worldwide concerning the impact of habitat loss, we know little concerning the relative impacts of the various forms of habitat loss presented in the literature. This includes the overarching term *habitat loss*, but more specifically *habitat degradation*, *habitat destruction* and *habitat fragmentation*. Facilitating this lack of understanding is a lack of consistency in the definitions used when studying these phenomena, leading to varying conclusions regarding the magnitude and direction of realized impacts. Somewhat ironically, it is agreed, or at least recognized by some, that this lack of consistency has indeed led to several issues when interpreting empirical results (Fahrig 2003; Jackson and Fahrig 2013). Furthermore, while highly focused research under one definition may yield useful insights, they can also be problematic in that they lead to oversights in other perspectives (Fischer and Lindenmayer 2007).

Unfortunately still, the issues found in the ecological literature has bled into the mathematical modelling literature. There have been a huge variety of models proposed to describe these various forms of habitat loss, with varying mechanisms used to describe the process of “lost” habitat, and so it is inevitable that these models do not all reach the same conclusions. One facilitator of this outcome is, again, the lack of consistency in what exactly constitutes habitat *degradation* versus habitat *fragmentation*, for example. Additionally, these models make varying assumptions about what aspects are most important in their construction, such as habitat loss as a patch-scale problem versus a landscape-scale problem, while some authors may dispute this distinction entirely (Fahrig 2013). Combining these two issues has resulted in a vast amount of modelling types and techniques with widely varying results and implications on the impact of habitat loss on species.

For these reasons, we will precisely state what we mean when referring to these occasionally ambiguous terms. It should be clear that we are not suggesting that one definition is better than another necessarily, but rather that it is important to be precise in our terminology so that all readers are on the same page. In this paper, we adhere to the following definitions.

Habitat Degradation A general term describing any set of processes resulting in a decrease in quality of habitat.

Habitat Destruction When a natural habitat is altered so dramatically that it no longer supports the species it originally sustained (Laurance 2010).

Habitat Fragmentation Changes in habitat configuration that result from the breaking apart of existing habitat, independent of habitat degradation and/or destruction.

Habitat Loss Any combination of one or more of the process of habitat degradation, destruction or fragmentation.

Sometimes, habitat loss is taken to be synonymous with habitat destruction. However, we feel that this equivalence can lead to confusion, as degraded habitat can also conceptually be considered “lost” habitat if its net impact is negative on the native species. Additionally, fragmentation is often considered as an implicit part of the overall process of habitat loss, but for modelling purposes, fragmentation should be considered as a distinct process from that of habitat destruction. The reason for this distinction comes back to the desire to understand the relative impacts of these differing processes, independent of one another. For these reasons, habitat loss is taken to mean any of the three processes described above.

Habitat degradation and destruction, as defined above, clearly reside on a spectrum. That is to say, severe habitat degradation could be argued as destruction, and minor amounts of habitat destruction could be considered as habitat degradation. However, we do believe that it is important to make the distinction between the two, as it is important to take into account the quality of the habitat and its impact on species (Heinrichsa et al. 2016). This will become more important upon introduction of the mathematical model to be discussed here.

Finally, for fragmentation, we have chosen to use the definition of fragmentation *per se* presented in (Fahrig 2003) or (Jackson and Fahrig 2013), as it avoids many

of the potential issues discussed thus far. That is, in making this distinction we are able to discuss the individual impacts of the amount of good (or bad) habitat and the configuration of said habitat. This is made more precise in the discussion section of our paper, though is outside the scope of the concrete conclusions drawn here. This leaves open an interesting direction for future research.

The goal of this paper is to introduce a spatially explicit competition-diffusion model, given as a system of partial differential equations, whose purpose is to understand the effect of habitat degradation on the persistence and extinction of two competing species. We hope to use the distinctions outlined thus far in order to more clearly define the factors and outcomes given by the modelling framework presented in the following section. While it may be impossible to disentangle the various forms of habitat loss in an empirical setting, it is reasonable to separate these effects in a simplified modelling setting. Aside from alleviating some of the confusion found in the literature, the framework presented in the following section demonstrates at least one way to distinguish these various forms of habitat loss and provides an avenue to further study both the individual as well as the combined effects of each. This leaves open areas for future research, which we make more concrete in the discussion section of this paper. The choice to refer to our model as describing degradation will become clear in its construction as follows.

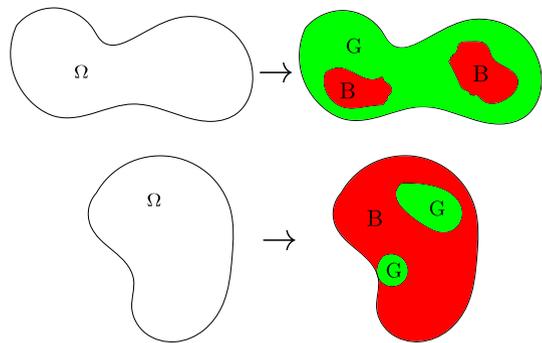
1.2 Model derivation

Consider a smooth (e.g. C^1), bounded domain $\Omega \subset \mathbb{R}^N$, $N \geq 1$, which we will treat as the entire available habitat for two competing species. We now introduce some heterogeneity in the environment which seeks to model the degradation of some portion of the habitat, or to be more precise, to model the variable effect on each species' population growth within the degraded portion of habitat. The assumptions made in this regard can be stated as follows:

- (i) The habitat is split into two regions such that $\Omega = G \cup B$. G denotes the undisturbed region(s), while B denotes the region(s) of degraded habitat. We always assume that $0 < |B| < |\Omega|$, where $|\cdot|$ denotes the Lebesgue measure.
- (ii) In region G , both populations grow as described by the standard Lotka-Volterra competition model (Cantrell and Cosner 2003; Murray 1989).
- (iii) In region B , both species experience only mortality, though not necessarily at the same rate.

Since our goal is to model the effect of habitat degradation on competing species, assumption (i) simply ensures that there are both good and bad regions within the available habitat (Fig. 1). Assumption (ii) should be clear, while assumption (iii) deserves some attention. Assumption (ii) assumes that two competing species interact as they normally would in the undisturbed regions. One could also consider other forms of interaction between two species in this region, such as a mutualistic model. This could be an interesting direction for further study, however we restrict ourselves to one type of interaction in this paper. Assumption (iii) implicitly assumes that the competing species do not interact in the degraded region B . This is more or less reasonable depending on the actual mechanism of competition. If the interference

Fig. 1 A two-dimensional representation of assumption (i), where the whole domain Ω is broken into disjoint subdomains representing the undisturbed region of habitat “G” and the degraded region of habitat “B”. The regions can be of any (fixed) shape or size, as long as both regions have positive area



competition occurs in order to maintain access to a specific resource, such as water or territory necessary for survival, it is assumed that the degraded region(s) do not contain such resources, and so competition is no longer necessary in these regions. Similarly, in the case of exploitative competition (i.e. competition which occurs indirectly between individuals), the use of a necessary resource by one species results in less resource for other species. In the degraded region(s), there are no such resources available, and so it is reasonable to assume that there is no competitive interaction. Point (iii) also introduces the concept of *resilience* in our model: an ability to withstand or recover quickly from difficult conditions. The species which experiences a smaller level of detriment in the degraded region is better able to withstand environmental changes when compared to their competitor. In this sense, the more resilient species is the stronger competitor.

If we denote by $\mathbb{1}_K$ the indicator function of a set $K \subset \mathbb{R}^N$, the habitat degradation model can be written as follows:

$$\begin{cases} u_t = d_1 \Delta u + \mathbb{1}_G u(1 - u - \gamma_1 v) - c_1 \mathbb{1}_B u & \text{in } \Omega \times (0, T), \\ v_t = d_2 \Delta v + \mathbb{1}_G v(1 - \gamma_2 u - v) - c_2 \mathbb{1}_B v & \text{in } \Omega \times (0, T). \end{cases}$$

Through this construction, we have split the domain into two (almost) disjoint regions—assumption (i). We see logistic growth and competition in the undisturbed habitat G , while both species experience mortality in region B at rates $c_i \geq 0$, $i = 1, 2$ —assumptions (ii) and (iii), respectively. For clarity, we assume the rate of competition is equal, i.e. $\gamma_1 = \gamma_2 = 1$, so as to isolate the effects of degradation on the interacting species alone. We consider species u as a slow diffuser and species v as a fast diffuser, that is, $d_1 \leq d_2$. This assumption has included all possibilities without loss of generality because the system is symmetric for the competing species. For the purpose of our analysis, we prescribe homogeneous Neumann boundary data along $\partial\Omega$.

The Neumann problem may now be more conveniently written as follows:

$$\begin{cases} u_t = d_1 \Delta u + u[m_{c_1} - \mathbb{1}_G(u + v)] & \text{in } \Omega \times (0, T), \\ v_t = d_2 \Delta v + v[m_{c_2} - \mathbb{1}_G(u + v)] & \text{in } \Omega \times (0, T), \\ \frac{\partial u}{\partial \mathbf{n}} = \frac{\partial v}{\partial \mathbf{n}} = 0 & \text{on } \partial\Omega \times (0, T), \end{cases} \tag{1.1}$$

where

$$m_{c_i} := \mathbb{1}_G - c_i \mathbb{1}_B, \quad i = 1, 2. \quad (1.2)$$

We now investigate the global dynamics of the system depending on the relation between the parameters d_i and c_i . In addition to the problem above, closely related is the scalar counterpart

$$\begin{cases} w_t = d\Delta w + w(m_c - \mathbb{1}_G w) & \text{in } \Omega \times (0, T), \\ \frac{\partial w}{\partial \mathbf{n}} = 0 & \text{on } \partial\Omega \times (0, T), \end{cases} \quad (1.3)$$

where $m_c = \mathbb{1}_G - c\mathbb{1}_B$ with $c \geq 0$, as well as the steady state problems associated with both (1.1) and (1.3). These are discussed in details in the following sections.

1.3 Comparisons to other work

We begin with comparison to existing habitat loss modelling efforts. First and foremost, it should be noticed that this model is spatially explicit, and so it explicitly captures the impact that the heterogeneity has on the competing species. As a comparison, one may consider a classic habitat loss model given in (Tilman et al. 1994) in which n species compete for a shared resource. The model is given as a system of ordinary differential equations, and is therefore spatially homogeneous. The species are ordered in terms of their competitiveness, i.e. superior species can occupy the area of inferior species, whereas inferior species cannot occupy the area held by a superior competitor. The destruction is described in terms of the proportion of available habitat remaining, i.e. the total available habitat is 1, and the proportion of available habitat is $1 - D$, where D is the proportion of total habitat that has been removed. Interestingly, such a construction leads to the counterintuitive result that as D increases from 0 to 1, the ordering of deterministic extinction is from the strongest to the weakest species. In particular, the superior species will always go extinct first under increasing habitat removal, a result which is at odds with what we see in nature (Klausmeier 1998; Lin and Liu 2006). This setup does not consider the effect (whether positive or negative) of configuration or fragmentation, as there is no distinction between possible configurations. Furthermore, this type of model is more accurately described as a habitat *destruction* model (as opposed to habitat *degradation* model), as the lost region is removed from the model entirely for all species, and so no consideration is given to the precise quality of the lost habitat. This framework introduced by Tilman et al. has been investigated extensively, including other effects not originally considered, such as variation in patch quality and the rescue effect (Gyllenberg and Hanski 1997) or the Allee effect (Chen and Hui 2009). In the first case, the study of variation in patch quality is closest to a degradation model in one sense, however this approach relies on a discrete spatial setting and hence lacks an inclusion of continuous spatial features and does not consider the combined effects of competition and degradation. Such constructions align more closely with the habitat amount hypothesis, see (Fahrig 2013).

More generally, it has been a popular approach to model habitat loss through metapopulations, or multiple patches, as introduced by Levins in 1969 (Levins 1969). Such modelling efforts vary in their construction, application and complexity, see for example, (Nee and May 1992; Hess 1996; Keymer et al. 2000) or more recently (McVinish et al. 2015). These models are mathematically similar to the ODE habitat loss model prototype described previously, and so suffer from similar drawbacks. However, even in the cases where the models differ (both mathematically and conceptually) in a more significant way, the precise measurement of “habitat loss” is often obscured, or at least inconsistent across modelling efforts. One may refer to (Jackson and Fahrig 2013), which highlights some of the measures that may be used in these contexts. This includes measures such as number of patches, mean patch size, mean patch isolation, or total edge amount. Depending on the modelling framework, any combination of these measures can be interpreted as habitat loss or fragmentation. This results in confusion, as highlighted by Figure 3 in (Jackson and Fahrig 2013). Roughly speaking, one can hold any variable fixed and alter the remaining variables positively or negatively in order to draw widely varying conclusions regarding the persistence of species. One benefit of using a spatially explicit model is that all of these factors are encapsulated within the model, with the drawback being an increased difficulty in performing analysis for any particularly chosen configuration. Such drawbacks may be overcome through the use of numerical simulation, however.

Some authors have proposed spatially explicit models comparable to that presented here (Strohm and Tyson 2012), however, the analysis involves simplifications in order to make comparisons to the spatially homogeneous ODE model. Such simplifications include an appeal to a one dimensional model only, dropping higher order terms and reducing to the form of an ordinary differential equation. Such efforts are valuable in determining the disparity between spatially homogeneous and spatially heterogeneous models, especially when it comes to using these models to inform decisions made in the area of conservation biology.

Our mathematical model (1.1) most closely resembles existing models investigating the effect of heterogeneous environments, see chapter 4 in (Ni 2001) and the references therein, and more recently (He and Ni 2015, 2016, 2017), which provide a rather complete picture of the global dynamics under fairly mild assumptions on the heterogeneity appearing in the system. However, these results rely on either positivity of the environmental heterogeneity (i.e. $m(x) \geq 0$), or require the average of the heterogeneity to be positive in the cases where it is allowed to change sign, which is much too restrictive for our setting. In addition, the existence of coexistence steady states are proven only for limiting cases where either $(d_1, d_2) \rightarrow (0^+, 0^+)$ or $(d_1, d_2) \rightarrow (\infty, \infty)$ while the environment is held fixed. In our setup, we are able to provide a complete description of the global dynamics in a way that removes some of this abstraction due to the particular choices of spatial heterogeneity. In this way, we provide a more detailed description of *environmental* impacts as opposed to impacts of dispersal rates alone. This leads to a more detailed understanding of the impact of habitat degradation in relation to diffusion rates and levels of resilience (parameters d_i and c_i , $i = 1, 2$), and even guarantees the existence of a stable coexistence steady state for a large parameter regime. One may also note that our approach requires a

consideration of the case when the environmental heterogeneity is discontinuous (but bounded), which does not satisfy the usual Hölder continuity assumption.

Additionally, readers are referred to some interesting results found in (Cantrell and Cosner 2003) where the authors consider a one dimensional habitat $(0, 1)$ with heterogeneity of the form

$$m_a(x) := \begin{cases} -1 & \text{for } x \in [0, a), \\ k & \text{for } x \in [a, a + L), \\ -1 & \text{for } x \in [a + L, 1]. \end{cases}$$

The authors investigate the optimal location of the favorable region given by the parameter a . This is done for both Dirichlet and Neumann boundary conditions, and a more general investigation is given in (Cantrell and Cosner 1989, 1991a,b). Such work provides some motivation and insight into the investigation presented here, but tends to focus on the particular locations of favorable habitat patches in single species models rather than the impact of the measure of detriment within the favorable and unfavorable regions.

We now investigate the long term behaviour and properties of the steady states corresponding to problem (1.1) depending on the parameters appearing within the model. In particular, we explore changes in stability based on the parameters c_i , which measures the effect of the degraded region on the competing species u and v .

1.4 Statement of main results

Denote by $C(\overline{\Omega})$ the space of continuous functions on $\overline{\Omega}$ equipped with the maximum norm. Denote by $C^+(\overline{\Omega})$ the positive cone of $C(\overline{\Omega})$, namely, $C^+(\overline{\Omega}) = \{f \in C(\overline{\Omega}) : f \geq 0 \text{ in } \overline{\Omega}\}$.

Denote by (u, v) the unique global strong solution to (1.1) with initial data $(u_0, v_0) \in (C^+(\overline{\Omega}) \setminus \{0\}) \times (C^+(\overline{\Omega}) \setminus \{0\})$. See Definition 3.1 for the definition of strong solutions and Theorem 3.1 for the well-posedness of the problem.

Denote by $\mu_1(d_1, m_{c_1})$ (resp. $\mu_1(d_2, m_{c_2})$) the principal eigenvalue associated with the linearization of (1.3) at 0 with $(d, m) = (d_1, m_{c_1})$ (resp. $(d, m) = (d_2, m_{c_2})$). See Proposition A.2.

Whenever $\mu_1(d_1, m_{c_1}) < 0$ (resp. $\mu_1(d_2, m_{c_2}) < 0$), denote by u^* (resp. v^*) the unique positive steady state of (1.3) with $(d, m) = (d_1, m_{c_1})$ (resp. $(d, m) = (d_2, m_{c_2})$). See Theorem 2.2.

The following is the main result of this paper.

Theorem 1.1 *Let $0 < d_1 < d_2$. Then the following hold (with all convergences hold in $C(\overline{\Omega}) \times C(\overline{\Omega})$).*

- (1) *Suppose $\mu_1(d_1, m_{c_1}) \geq 0$ and $\mu_1(d_2, m_{c_2}) \geq 0$. Then, $(u, v) \rightarrow (0, 0)$ as $t \rightarrow \infty$.*
- (2) *Suppose $\mu_1(d_1, m_{c_1}) < 0$ and $\mu_1(d_2, m_{c_2}) \geq 0$. Then, $(u, v) \rightarrow (u^*, 0)$ as $t \rightarrow \infty$.*
- (3) *Suppose $\mu_1(d_1, m_{c_1}) \geq 0$ and $\mu_1(d_2, m_{c_2}) < 0$. Then, $(u, v) \rightarrow (0, v^*)$ as $t \rightarrow \infty$.*

- (4) Suppose $\mu_1(d_1, m_{c_1}) < 0$ and $\mu_1(d_2, m_{c_2}) < 0$. Then, there exist critical values $0 < \underline{c}_2^* < \bar{c}_2^* < c_1$ such that the following results hold.
- (i) If $c_2 \in (\bar{c}_2^*, \infty)$, then $(u, v) \rightarrow (u^*, 0)$ as $t \rightarrow \infty$.
 - (ii) If $c_2 \in (\underline{c}_2^*, \bar{c}_2^*)$, then $(u, v) \rightarrow (\tilde{u}, \tilde{v})$ as $t \rightarrow \infty$, where (\tilde{u}, \tilde{v}) is the unique coexistence steady state of (1.1).
 - (iii) If $c_2 \in (0, \underline{c}_2^*)$, then $(u, v) \rightarrow (0, v^*)$ as $t \rightarrow \infty$.

Furthermore, \underline{c}_2^* and \bar{c}_2^* are given by the unique zero of the functions $c_2 \mapsto \mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*)$ and $c_2 \mapsto \mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*)$, respectively. That is,

$$c_2 = \underline{c}_2^* \iff \mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*) = 0,$$

and

$$c_2 = \bar{c}_2^* \iff \mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*) = 0.$$

Remark 1.2 Note that in the description of \underline{c}_2^* , the dependence of $\mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*)$ on c_2 is given implicitly by the dependence of v^* on c_2 . This is in contrast to \bar{c}_2^* where the dependence is more explicit, seen directly by m_{c_2} .

The proof of Theorem 1.1 is given in Sect. 3.3. Points (1)–(3) follow rather directly from the comparison principle and the global dynamics of the scalar equation (see Theorem 2.2). Point (4) is much more delicate. This result follows from sharp results on the linearized stability of $(u^*, 0)$ and $(0, v^*)$ (see Lemmas 3.3 and 3.4, respectively), the stability of all any coexistence state (see Lemma 3.5), the ordering of \underline{c}_2^* and \bar{c}_2^* (see Lemma 3.6), and finally a result from the theory of monotone flows (see Proposition 3.2).

Although the conditions above are implicit, given by the sign of a particular eigenvalue, the biological interpretation can be made quite clear. In case (1), two positive eigenvalues indicates that neither species can survive on its own, let alone in the presence of a competitor. In this case, it is intuitive that both species should go extinct in the presence of the other. Cases (2) and (3) indicate that if one species cannot survive on its own while the other species can, the species that *can* survive on its own will persist despite the presence of a competitor. This result is also biologically intuitive. Most interesting is case (4), which demonstrates the trade off between the rate of diffusion and the level of resilience within the degraded region B . Here, two negative eigenvalues assumes that both species can survive in the absence of a competitor. The interesting consequence is that, depending on the level of detriment each species experiences in the degraded region B , one or both species may survive. Point (4)(i) demonstrates that a minor amount of competitive advantage in the degraded region is not enough to overcome the advantage gained by the slower rate of diffusion. Note that it is generally understood that a slower rate of diffusion is advantageous in competition-diffusion models, the phenomenon known as “*the slower diffuser always wins*” (Dockery et al. 1998; Ni 2001), at least when the environmental heterogeneity is constant in time. When there are both good (positive) and bad (negative) regions, the advantage of slower diffusion can be understood as a result of less loss of individuals in the degraded region. However, this result holds even when the environment

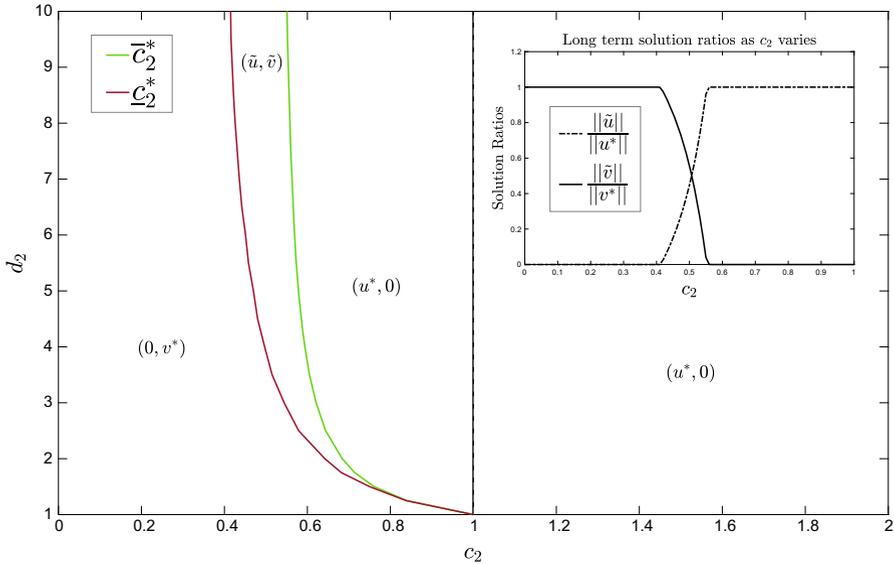


Fig. 2 A region plot showing the long term behaviour of solutions in the c_2 - d_2 plane. We fix $d_1 = c_1 = 1$; the black vertical line denotes $c_1 = 1$. The habitat is given by $\Omega = (0, 10)$, $G = (0, 4) \cup (6, 10)$, $B = (4, 6)$. The quantities \bar{c}_2^* , \bar{c}_2^* are the quantities defined in Theorem 1.1. The subplot is a cross section of the case when $d_2 = 10$, where the time dependent solution is compared to the respective competition independent steady state after a sufficiently large amount of time has passed to reach a steady state

is strictly positive and so there may be other possible mechanisms behind this phenomenon. Point (4)(ii) shows that coexistence is possible if the trade off between the diffusion speed and the level of detriment is intermediate. Perhaps most importantly, point (4)(iii) demonstrates that it is possible to overcome the advantage gained by a slower rate of diffusion through advantage in the degraded region alone. To clarify this point further, notice that while both populations decay in the degraded region, an advantage can be gained through resilience, that is, a *smaller* rate of decay in comparison to the other species.

Below, Fig. 2 and the related subplot capture points 4(i)–(iii) of the main theorem. \bar{u} , \bar{v} denote the time dependent solution after enough time has passed such that it has reached equilibrium. u^* , v^* denote the competition independent solutions, both of which exist in the chosen parameter regimes. The norm used is $L^1(\Omega)$. There is a wide range of c_2 for coexistence, and we can make the coexistence window even wider if the degraded region has a less negative effect on both species.

In addition, we have the following limiting case relating to point (iii) in Theorem 1.1.

Theorem 1.3 *Let $0 < d_1 < d_2$ and $c_2 = 0 < c_1$. Then,*

$$(u, v) \rightarrow (0, v^*) \text{ in } C(\bar{\Omega}) \times C(\bar{\Omega}) \text{ as } t \rightarrow \infty.$$

The proof of Theorem 1.3 also appears in Sect. 3.3, subsequent to the proof of Theorem 1.1. The proof follows from the same arguments made in the proof of Theorem 1.1 point (4), but in the special case where $c_2 = 0$.

This result is of notable significance due to its implications for the sustainability of multiple species. This result suggests that, under the introduction of any amount of degraded habitat, if one species is particularly resilient in the degraded region, not only will it survive, but it will drive the other species to extinction! Moreover, this result holds for any such $0 < d_1 < d_2$. Hence, under the introduction of differing environmental heterogeneity between the two species, the slower diffuser may not always win! In fact, in the limiting case, as long as species u experiences some level of mortality in some region of Ω , species v always drives species u to extinction! The remarkable fact is that this holds for any $c_1 > 0$, for any region B , regardless of how small c_1 or the region B might be.

Below are some consequences of existing results, providing a more complete picture of the overall dynamics of the system.

Theorem 1.4 *Suppose that $d_1, d_2 > 0$ and $c_1 = c_2 = 0$. Then, there exists a curve of steady states of the form $\{(\sigma, 1 - \sigma) : \sigma \in [0, 1]\}$. Furthermore, the linearization about the semitrivial steady states $(1, 0)$ and $(0, 1)$ have a zero eigenvalue.*

Proof In this case, our system becomes

$$\begin{cases} u_t = d_1 \Delta u + \mathbb{1}_G u(1 - u - v), \\ v_t = d_2 \Delta v + \mathbb{1}_G v(1 - u - v). \end{cases}$$

Clearly, constant steady states consist of $\{(\sigma, 1 - \sigma) : \sigma \in [0, 1]\}$. Linearizing about the steady state $(u^*, 0) = (1, 0)$ gives

$$\begin{cases} d_1 \Delta \psi_1 - \mathbb{1}_G \psi_1 - \mathbb{1}_G \psi_2 + \lambda \psi_1 = 0, \\ d_2 \Delta \psi_2 + \lambda \psi_2 = 0. \end{cases}$$

Obviously, $\lambda = 0$ is an eigenvalue with an eigenfunction $(\psi_1, \psi_2) = (1, -1)$. The same argument applies to $(0, v^*) = (0, 1)$, showing this state also has a zero eigenvalue. \square

Theorem 1.5 *Suppose that $d_1 = d_2 > 0$, and u^* and v^* exist. The following hold.*

- (1) *If $c_1 < c_2$, then $(u, v) \rightarrow (u^*, 0)$ in $C(\bar{\Omega}) \times C(\bar{\Omega})$ as $t \rightarrow \infty$.*
- (2) *If $c_1 > c_2$, then $(u, v) \rightarrow (0, v^*)$ in $C(\bar{\Omega}) \times C(\bar{\Omega})$ as $t \rightarrow \infty$.*

Proof The proof is identical to the case when $c_1 = c_2$ and $d_1 < d_2$. More precisely, the result follows from the monotonicity of the eigenvalue $\mu_1(d, m_c)$ with respect to c . \square

2 The scalar equation

In this section, we study the scalar Eq. (1.3) with $c \geq 0$ in preparation for the investigation of the system (1.1).

2.1 Well-posedness and global dynamics

We start with the definition of strong solutions and steady states to (1.3).

Definition 2.1 (1) A *strong solution* on $[0, T)$ to (1.3) is a solution which belongs to $W_p^{2,1}(\Omega \times (0, T)) \cap C([0, T); C(\overline{\Omega}))$ for all $p \geq 1$, satisfies the equation almost everywhere in $\Omega \times (0, T)$ and satisfies the boundary condition everywhere on $\partial\Omega$ for all $t \in (0, T)$. A *global strong solution* is a strong solution on $[0, T)$ for all $T > 0$.

(2) A *steady state* to (1.3) is a solution which belongs to $W^{2,p}(\Omega)$ for all $p \geq 1$, satisfies the equation almost everywhere in Ω and satisfies the boundary condition everywhere on $\partial\Omega$.

Remark 2.1 Since we may choose p as large as we like, the boundary condition is satisfied in the classical sense due to the Sobolev embedding.

Denote by $C^{++}(\overline{\Omega})$ the interior of $C^+(\overline{\Omega})$, namely, $C^{++}(\overline{\Omega}) = \{w \in C(\overline{\Omega}) : w > 0 \text{ on } \overline{\Omega}\}$. For $w^1, w^2 \in C(\overline{\Omega})$, we write $w^1 \ll w^2$ if $w^2 - w^1 \in C^{++}(\overline{\Omega})$.

We state the following comparison principle whose proof, being much simpler than that of Proposition 3.1, is omitted.

Proposition 2.1 Suppose $w^1, w^2 \in W_p^{2,1}(\Omega \times (0, T)) \cap C([0, T); C(\overline{\Omega}))$ for any $p \geq 1$, and satisfy

$$\begin{cases} w_t^1 \leq d\Delta w^1 + w^1(m_c - \mathbb{1}_G w^1) & \text{a.e. in } \Omega \times (0, T), \\ \frac{\partial w^1}{\partial \mathbf{n}} \leq 0 & \text{on } \partial\Omega \times (0, T), \\ w_t^2 \geq d\Delta w^2 + w^2(m_c - \mathbb{1}_G w^2) & \text{a.e. in } \Omega \times (0, T), \\ \frac{\partial w^2}{\partial \mathbf{n}} \geq 0 & \text{on } \partial\Omega \times (0, T). \end{cases}$$

- (1) If $w^1(\cdot, 0) \leq w^2(\cdot, 0)$, then $w^1(\cdot, t) \leq w^2(\cdot, t)$ for all $t \in (0, T)$.
- (2) Suppose, in addition, $w^1, w^2 \in C^1((0, T); C(\overline{\Omega}))$. If $w^1(\cdot, 0) \leq w^2(\cdot, 0)$ and $w^1(\cdot, 0) \not\equiv w^2(\cdot, 0)$, then $w^1(\cdot, t) \ll w^2(\cdot, t)$ for all $t \in (0, T)$.

Similarly, we have the following comparison theorem for nonnegative steady states.

Proposition 2.2 Suppose $w^1, w^2 \in W^{2,p}(\Omega)$ for any $p \geq 1$ are nonnegative and satisfy

$$\begin{cases} -d\Delta w^1 \leq w^1(m_c - \mathbb{1}_G w^1) & \text{a.e. in } \Omega, \\ \frac{\partial w^1}{\partial \mathbf{n}} \leq 0 & \text{on } \partial\Omega, \\ -d\Delta w^2 \geq w^2(m_c - \mathbb{1}_G w^2) & \text{a.e. in } \Omega, \\ \frac{\partial w^2}{\partial \mathbf{n}} \geq 0 & \text{on } \partial\Omega. \end{cases}$$

Then, $w^1 \leq w^2$. Moreover, there holds either $w^1 < w^2$ or $w^1 \equiv w^2$.

Proof Suppose that $w^1 \leq w^2$ were false. Set $\alpha^* := \inf \{ \alpha > 1 : w^1 \leq \alpha w^2 \}$. The continuity of w^1 and w^2 implies that $\alpha^* > 1$ and $w^1 \leq \alpha^* w^2$, and that there exists a point $x_0 \in \bar{\Omega}$ such that $w^1(x_0) = \alpha^* w^2(x_0)$.

Since $f(x, w) := w(m_c(x) - \mathbb{1}_G(x)w)$ satisfies $\alpha^* f(\cdot, w) \geq f(\cdot, \alpha^* w)$ for $w > 0$, we find $-d\Delta(\alpha^* w^2) \geq f(x, \alpha^* w^2)$. In particular, w^1 and $\alpha^* w^2$ are an ordered sub/super solution pair.

If $x_0 \in \Omega$, the strong maximum principle (Arena 1972, Theorem 1) implies that $w^1 \equiv \alpha^* w^2$ in Ω . Then, $0 < w^2 < w^1$ due to $\alpha^* > 1$, and hence, $0 = -d\Delta(w^1 - \alpha^* w^2) \leq \mathbb{1}_G w^1 (w^2 - w^1) < 0$ in G , a contradiction. If $x_0 \in \partial\Omega$, Hopf’s lemma gives $\frac{\partial}{\partial \mathbf{n}} (w^1 - \alpha^* w^2) > 0$ at x_0 , in contradiction to the boundary conditions assumed.

Hence, $w^1 \leq w^2$. Repeating the previous steps using the maximum principle and Hopf’s lemma, we find that either $w^1 < w^2$ or $w^1 \equiv w^2$ in $\bar{\Omega}$. This completes the proof. □

We now prove the following theorem concerning the well-posedness and global dynamics of (1.3). Recall that $\mu_1(d, m_c)$ is the principal eigenvalue associated with the linearization of (1.3) at 0.

Theorem 2.2 *For any initial data $w_0 \in C^+(\bar{\Omega})$, (1.3) admits a unique global strong solution $w \in C^\alpha([0, \infty); C^+(\bar{\Omega})) \cap C^1((0, \infty); C^+(\bar{\Omega}))$ for any $\alpha \in (0, 1)$. Furthermore, the following stability result holds.*

- (i) *Suppose $\mu_1(d, m_c) < 0$. Then, there exists a unique positive steady state $w_{d,c}^*$ to (1.3) and $w(\cdot, t) \rightarrow w_{d,c}^*$ in $C(\bar{\Omega})$ as $t \rightarrow \infty$ if $w_0 \not\equiv 0$.*
- (ii) *Suppose $\mu_1(d, m_c) \geq 0$. Then, $w(\cdot, t) \rightarrow 0$ in $C(\bar{\Omega})$ as $t \rightarrow \infty$.*

This theorem says that as long as the degraded regions are not *too* detrimental to the species, the population will persist. The following proof is included for completeness, but essentially follows from classical results, standard L^p -theory of elliptic and parabolic equations, Propositions 2.1 and 2.2 and the theory of monotone flows. In what follows, $Q_T := \Omega \times (0, T)$ for $T > 0$.

Proof of Theorem 2.2 Note that the uniqueness of global strong solutions follows immediately from Proposition 2.1. We show the existence. First, we may approximate m_c and $\mathbb{1}_G$ by functions m_c^ε and $\mathbb{1}_G^\varepsilon$ belonging to $C^\infty(\Omega)$, and so that $m_c^\varepsilon \rightarrow m$ and $\mathbb{1}_G^\varepsilon \rightarrow \mathbb{1}_G$ in $L^p(\Omega)$ for any $p \geq 1$. By classical parabolic theory (see e.g. Wu et al. 2006, Chapter 8), for each $\varepsilon > 0$ there exists a unique, positive classical solution w_ε . It is easy to show that the solution w_ε is uniformly bounded in ε with respect to $L^\infty(\Omega)$, and so by standard L^p theory of parabolic equations (see e.g. Wu et al. 2006, Chapter 9), w_ε is uniformly bounded in $W_p^{2,1}(Q_T)$ for any $p > 1$. Taking $\varepsilon \rightarrow 0$, up to subsequence if necessary, we conclude that $w_\varepsilon \rightarrow w$ in $W_p^{2,1}(Q_T)$ and this limit function w is a strong solution to problem (1.3). Furthermore, by the Sobolev embedding, $w \in C^{1+\alpha, (1+\alpha)/2}(\bar{Q}_T)$ for any $\alpha \in (0, 1)$. Then, since it is easily shown that solutions are exponentially bounded, this solution is in fact global. In particular, $w \in C^{(1+\alpha)/2}([0, \infty); C(\bar{\Omega}))$. The regularity of w is an immediate consequence of (Stewart 1980, Theorem 3). Indeed, since $w_0 \in C^+(\bar{\Omega})$ and

$(x, t) \mapsto w(x, t)(m_c(x) - \mathbb{1}_G w(x, t))$ is Hölder continuous in time, $\frac{\partial w}{\partial t}$ exists and is uniformly continuous on $(0, \infty) \times \bar{\Omega}$. Hence, $w \in C^1((0, \infty); C(\bar{\Omega}))$.

We verify that w satisfies the Neumann boundary condition. Since $w_\varepsilon \rightarrow w$ in $C^{1+\alpha}(\bar{\Omega})$ as $\varepsilon \rightarrow 0$, we see for any fixed $t > 0$ and $x_0 \in \partial\Omega$

$$\begin{aligned} \left| \frac{\partial w}{\partial \mathbf{n}}(x_0, t) \right| &\leq \left| \frac{\partial}{\partial \mathbf{n}}(w(x_0, t) - w_\varepsilon(x_0, t)) \right| + \left| \frac{\partial w_\varepsilon}{\partial \mathbf{n}}(x_0, t) \right| \\ &= \left| \lim_{x \rightarrow x_0} \frac{(w - w_\varepsilon)(x_0, t) - (w - w_\varepsilon)(x, t)}{x - x_0} \right| \leq \|w - w_\varepsilon\|_{C^1(\bar{\Omega})}. \end{aligned}$$

Taking $\varepsilon \rightarrow 0$ shows that $\frac{\partial w}{\partial \mathbf{n}} = 0$ for all $x \in \partial\Omega$ and $t > 0$.

The convergence results follow from standard arguments (see e.g. (Hess 1991; Zhao 2017)). We include the arguments below for the sake of completeness. Denote by $\{\Phi_t\}_{t \geq 0}$ the semiflow on $C^+(\bar{\Omega})$ generated by solutions of (1.3). Let $u_0 \in C^+(\bar{\Omega}) \setminus \{0\}$. Replacing u_0 by $\Phi_1 u_0$, we may assume without loss of generality that $u_0 \in C^{++}(\bar{\Omega})$.

When $\mu_1(d, m_c) < 0$, (1.3) admits a unique positive steady state $w_{d,m}^*$. Indeed, denote by ϕ_1 the positive eigenfunction associated with $\mu_1(d, m_c)$. Direct computations verify that $\varepsilon\phi_1$ is a sub solution for all small ε , and each $M \gg 1$ is a super solution. Fix ε so small and M so large that $\varepsilon\phi_1 \leq u_0 \leq M$. Then, $\Phi_t(\varepsilon\phi_1) \leq \Phi_t u_0 \leq \Phi_t M$ for all $t \geq 0$ thanks to Proposition 2.1. Moreover, $\Phi_t(\varepsilon\phi_1)$ is increasing in t and converges pointwise to the positive steady state \underline{w}_{d,m_c}^* as $t \rightarrow \infty$, and $\Phi_t M$ is decreasing in t and converges pointwise to a positive steady state $\overline{w}_{d,c}^*$ as $t \rightarrow \infty$. Proposition 2.2 guarantees that $\underline{w}_{d,c}^* = \overline{w}_{d,c}^*$, that is, the steady state denoted by $w_{d,c}^*$ is unique. By Dini’s theorem, the convergence holds in $C(\bar{\Omega})$. It follows that $\Phi_t u_0 \rightarrow w_{d,c}^*$ in $C(\bar{\Omega})$ as $t \rightarrow \infty$.

If $\mu_1(d, m_c) \geq 0$, then 0 is the only steady state to (1.3). Indeed, it follows that for each $M \gg 1$, $\Phi_t M$ is decreasing in t and converges in $C(\bar{\Omega})$ to 0 as $t \rightarrow \infty$. Fixing M so large that $u_0 \leq M$, we conclude that $\Phi_t u_0 \rightarrow 0$ in $C(\bar{\Omega})$ as $t \rightarrow \infty$. This completes the proof. \square

From this result, we see that persistence depends intimately on m_c . Since $m_c = \mathbb{1}_G - c \mathbb{1}_B$, the persistence of a single species depends on the size of the region B and the level of resilience (described by the parameter c) within region B . In particular, given any size or location of destroyed habitat, one can always choose c sufficiently small such that $\int_\Omega m dx = |G| - c|B| > 0$ so long as $|G| > 0$ (see Lemma 2.3). This implies that given any configuration of good and bad regions, there is always a value c sufficiently small such that the species’ population persists. Notice that the same cannot be said concerning extinction if we take c large!

This motivates consideration of the special case when $c = 0$. In this case, our nonlinear term becomes $w(\mathbb{1}_G - \mathbb{1}_G w) = \mathbb{1}_G w(1 - w)$. In this form, $w \equiv 1$ is the only steady state, and hence, $w \rightarrow 1$ as $t \rightarrow \infty$ for any nontrivial initial data. This is an interesting result as it indicates that as long as there is *some* region where the growth rate of the species is positive (in this case, in the region G at rate 1), the species will reach carrying capacity *everywhere*. This point will become important later when discussing a similar limiting case of the full system (1.1).

2.2 Some useful results

In this section we present some results for later use.

Lemma 2.3 *There exists $c^* = c^*(d) \in (0, \infty]$ such that $\mu_1(d, m_c) < 0$ if and only if $c \in [0, c^*)$.*

Proof Direct computation shows that $\int_{\Omega} m_c = |G| - c|B| \geq 0$ for all $0 \leq c \leq \frac{|G|}{|B|}$. It follows from Proposition A.2 (i) that $\mu_1(d, m_c) < 0$ for all $c \in [0, \frac{|G|}{|B|}]$.

By Proposition A.2 (iv) and (v), the function $c \mapsto \mu_1(d, m_c)$ is increasing and continuous on $[0, \infty)$. Thus, if $\lim_{c \rightarrow \infty} \mu_1(d, m_c) > 0$, then there is a unique $c^* \in (0, \infty)$ such that $\mu_1(d, m_c) = 0$ when $c = c^*$, and $\mu_1(d, m_c) < 0$ if and only if $c \in [0, c^*)$. If $\lim_{c \rightarrow \infty} \mu_1(d, m_c) \leq 0$, then $\mu_1(d, m_c) < 0$ for all $c \in [0, \infty)$. In this case, $c^* = \infty$. □

Let $c^* = c^*(d)$ be as in Lemma 2.3. Theorem 2.2 ensures that (1.3) admits a unique positive steady state $w_{d,c}^*$ for each $c \in [0, c^*)$. We prove the following result.

Lemma 2.4 *There hold $w_{d,c}^* < 1$ in $\bar{\Omega}$ for all $c \in (0, c^*)$. Furthermore, $w_{d,c}^* \rightarrow 1$ in $C(\bar{\Omega})$ as $c \rightarrow 0$.*

Proof We write w_c^* for $w_{d,c}^*$ for notational simplicity.

Notice that $w_0^* \equiv 1$. Then, for any $c \in (0, c^*)$, $w_c^* \leq 1$ by Proposition 2.2. The strong maximum principle for strong solutions (see e.g. Arena 1972, Theorem 1) then implies that $w_c^* < 1$ in Ω . If $w_c^*(x_0) = 1$ for some $x_0 \in \partial\Omega$, Hopf’s lemma implies that $\frac{\partial w_c^*}{\partial \mathbf{n}}(x_0) > 0$, which contradicts the boundary condition satisfied by w_c^* , and so $w_c^* < 1$ in $\bar{\Omega}$ for all $c \in (0, c^*)$.

By Proposition 2.2, w_c^* is increasing as c decreases. Hence, the pointwise limits $w^* := \lim_{c \rightarrow 0} w_c^*$ exist in $\bar{\Omega}$, and $0 < w^* \leq 1$ in $\bar{\Omega}$. The auxiliary function $z_c := 1 - w_c^* \geq 0$ satisfies

$$-d\Delta z_c = -w_c^*(m_c - \mathbb{1}_G w_c^*) \quad \text{a.e. in } \Omega. \tag{2.1}$$

Multiplying the above equation by z_c , integrating over Ω and integrating by parts yield $d \int_{\Omega} |\nabla z_c|^2 dx = - \int_{\Omega} z_c w_c^*(m_c - \mathbb{1}_G w_c^*) dx$. As $m_c = \mathbb{1}_G - c \mathbb{1}_B$, we find

$$d \int_{\Omega} |\nabla z_c|^2 dx = - \int_G z_c^2 w_c^* dx + c \int_B z_c w_c^* dx \leq c \int_B z_c w_c^* dx \leq c|B|.$$

Hence, $\|\nabla z_c\|_{L^2(\Omega)} \rightarrow 0$ as $c \rightarrow 0$. Since $z_c \in C^{1,\alpha}(\bar{\Omega})$, ∇z_c exists in the classical sense and is uniformly bounded in c . Indeed, the Sobolev embedding guarantees that $\|z_c\|_{C^1(\bar{\Omega})} \leq M \|z_c\|_{W^{2,p}(\Omega)}$ for some constant $M > 0$. Since the right hand side of the equation satisfied by z_c is uniformly bounded in L^p for any $p \geq 1$, $\|z_c\|_{W^{2,p}(\Omega)}$ is uniformly bounded by standard elliptic L^p estimates. This together with Hölder’s inequality and the convergence in $L^2(\Omega)$ implies that $\|\nabla z_c\|_{L^p(\Omega)} \rightarrow 0$ for any $p \geq 1$.

From previous arguments, the right hand side of (2.1) is uniformly bounded in $L^p(\Omega)$ for $c \in (0, c^*)$ for any $p \geq 1$. Standard L^p estimates imply that z_c is uniformly

bounded in $W^{2,p}(\Omega)$, and compactness gives us the existence of a subsequence $\{c_k\}_k$ so that $z_{c_k} \rightarrow z_0$ in $W^{1,p}(\Omega)$ as $k \rightarrow \infty$. Then, since the right hand side of (2.1) consists only of lower order terms, the same L^p estimates imply that $z_c \rightarrow z_0$ in $W^{2,p}(\Omega)$. Consequently, for almost every $x \in \Omega$, we see that z_0 must satisfy

$$\begin{aligned} -d\Delta z_0 &= -d\Delta(z_0 - z_c) - d\Delta z_c = -d\Delta(z_0 - z_c) - w_c^*(m_c - \mathbb{1}_G w_c^*) \\ &= -d\Delta(z_0 - z_c) - \mathbb{1}_G w_c^* z_c + c \mathbb{1}_B (w_c^*)^2. \end{aligned}$$

Taking $c \rightarrow 0$, up to subsequence if necessary, yields $-d\Delta z_0 = -\mathbb{1}_G w_0^* z_0 \leq 0$, where the convergence is understood in the sense of $L^p(\Omega)$. The maximum principle implies that $z_0 = 0$ a.e. in Ω . The Sobolev embedding ensures that z_0 is in fact continuous, and so $z_0 = 0$ everywhere in Ω . Consequently, $z_c \rightarrow z_0 \equiv 0$ in $L^p(\Omega)$. The Sobolev embedding allows us to conclude that for p appropriately large, $\|z_c\|_{C(\overline{\Omega})} \leq M \|z_c\|_{W^{1,p}(\Omega)} \rightarrow 0$ as $c \rightarrow 0$. This implies that $w_c^* \rightarrow 1$ uniformly in $\overline{\Omega}$, completing the proof. \square

3 The system

In this section, we study the system (1.1) and prove our main results, Theorems 1.1 and 1.3.

3.1 Comparison principles

In what follows, the orderings $\leq_K, <_K$ and \ll_K denote the standard skew orderings for competitive systems: for $u_1, u_2, v_1, v_2 \in C(\overline{\Omega})$,

$$\begin{aligned} (u_1, v_1) \leq_K (u_2, v_2) &\text{ iff } u_2 - u_1 \in C^+(\overline{\Omega}) \text{ and } v_1 - v_2 \in C^+(\overline{\Omega}), \\ (u_1, v_1) <_K (u_2, v_2) &\text{ iff } u_2 - u_1 \in C^+(\overline{\Omega}) \setminus \{0\} \text{ and } v_1 - v_2 \in C^+(\overline{\Omega}) \setminus \{0\}, \\ (u_1, v_1) \ll_K (u_2, v_2) &\text{ iff } u_2 - u_1 \in C^{++}(\overline{\Omega}) \text{ and } v_1 - v_2 \in C^{++}(\overline{\Omega}). \end{aligned}$$

Proposition 3.1 *Let $T \in (0, \infty)$. Suppose that $\underline{u}, \overline{u}, \underline{v}, \overline{v}$ belong to $W_p^{2,1}(\Omega \times (0, T)) \cap C([0, T]; C(\overline{\Omega}))$ for any $p \geq 1$ with $\overline{u}(\cdot, 0), \overline{v}(\cdot, 0) \geq 0$ and satisfy the conditions:*

$$\begin{aligned} \underline{u}_t - d_1 \Delta \underline{u} &\leq \underline{u}(m_{c_1} - \mathbb{1}_G(\underline{u} + \overline{v})) \text{ a.e. in } \Omega \times (0, T), \\ \underline{v}_t - d_2 \Delta \underline{v} &\leq \underline{v}(m_{c_2} - \mathbb{1}_G(\overline{u} + \underline{v})) \text{ a.e. in } \Omega \times (0, T), \\ \overline{u}_t - d_1 \Delta \overline{u} &\geq \overline{u}(m_{c_1} - \mathbb{1}_G(\overline{u} + \underline{v})) \text{ a.e. in } \Omega \times (0, T), \\ \overline{v}_t - d_2 \Delta \overline{v} &\geq \overline{v}(m_{c_2} - \mathbb{1}_G(\underline{u} + \overline{v})) \text{ a.e. in } \Omega \times (0, T), \\ \frac{\partial \underline{u}}{\partial \mathbf{n}} &\leq \frac{\partial \overline{u}}{\partial \mathbf{n}} \text{ on } \partial\Omega \times (0, T), \\ \frac{\partial \underline{v}}{\partial \mathbf{n}} &\leq \frac{\partial \overline{v}}{\partial \mathbf{n}} \text{ on } \partial\Omega \times (0, T). \end{aligned}$$

Then, the following hold.

- (1) If $(\underline{u}(\cdot, 0), \bar{v}(\cdot, 0)) \leq_K (\bar{u}(\cdot, 0), \underline{v}(\cdot, 0))$, then $(\underline{u}(\cdot, t), \bar{v}(\cdot, t)) \leq_K (\bar{u}(\cdot, t), \underline{v}(\cdot, t))$ for all $t \in (0, T)$.
- (2) Suppose in addition $\underline{u}, \bar{u}, \underline{v}, \bar{v}$ belong to $C^1((0, \infty); C(\bar{\Omega}))$. If $(\underline{u}(\cdot, 0), \bar{v}(\cdot, 0)) <_K (\bar{u}(\cdot, 0), \underline{v}(\cdot, 0))$, then

$$(\underline{u}(\cdot, t), \bar{v}(\cdot, t)) \ll_K (\bar{u}(\cdot, t), \underline{v}(\cdot, t)), \quad \forall t \in (0, T).$$

Proof (1) First, we claim that $\bar{u}, \bar{v} \geq 0$ holds necessarily. Consider $w = -\bar{u}$. Then by assumption, w satisfies

$$w_t - d_1 \Delta w \leq \beta(t)w, \tag{3.1}$$

for some nonnegative $\beta(t)$, the existence of which follows from $\underline{v}, \bar{u} \in C([0, T]; C(\bar{\Omega}))$. Set $w^- = \max\{0, -\bar{u}\}$. Multiplying (3.1) by w^- , integrating the resulting inequality over Ω and integrating by parts yields that $\frac{1}{2} \frac{d}{dt} \int_{\Omega} (w^-)^2 dx \leq \beta(t) \int_{\Omega} (w^-)^2 dx$. From the Gronwall inequality and the nonnegativity at $t = 0$, we obtain $w^- \equiv 0$. The same argument applies to \bar{v} , and hence $\bar{u}, \bar{v} \geq 0$.

Now, set $w_1 := \underline{u} - \bar{u}$ and $w_2 = \underline{v} - \bar{v}$. We show that $w_i^+ := \max\{0, w_i\} \equiv 0$ for $i = 1, 2$. Setting $f_1(x, u, v) = u(m_{c_1} - \mathbb{1}_G(u + v))$ and $f_2(x, u, v) = v(m_{c_2} - \mathbb{1}_G(u + v))$, we estimate

$$\begin{aligned} & \frac{1}{2} \frac{d}{dt} \int_{\Omega} [(w_1^+)^2 + (w_2^+)^2] dx \\ & \leq \int_{\Omega} w_1^+ (d_1 \Delta w_1 + f_1(x, \underline{u}, \bar{v}) - f_1(x, \bar{u}, \underline{v})) dx \\ & \quad + \int_{\Omega} w_2^+ (d_2 \Delta w_2 + f_2(x, \bar{u}, \underline{v}) - f_2(x, \bar{u}, \underline{v})) dx \\ & \leq \int_{\Omega} w_1^+ (f_1(x, \underline{u}, \bar{v}) - f_1(x, \bar{u}, \underline{v})) dx \\ & \quad + \int_{\Omega} w_2^+ (f_2(x, \bar{u}, \underline{v}) - f_2(x, \bar{u}, \underline{v})) dx, \end{aligned} \tag{3.2}$$

where we used the assumed differential inequalities in the first inequality, and integrated by parts and dropped non-positive terms in the second inequality.

We now write

$$\begin{aligned} f_1(x, \underline{u}, \bar{v}) - f_1(x, \bar{u}, \underline{v}) &= \underline{u}(m_{c_1} - \mathbb{1}_G(\underline{u} + \bar{v})) - \bar{u}(m_{c_1} - \mathbb{1}_G(\bar{u} + \underline{v})) \\ &= m_{c_1}(\underline{u} - \bar{u}) - \mathbb{1}_G((\underline{u} + \bar{u})(\underline{u} - \bar{u}) + \bar{v}(\underline{u} - \bar{u}) - \bar{u}(\underline{v} - \bar{v})) \\ &= (m_{c_1} - \mathbb{1}_G(\underline{u} + \bar{u} + \bar{v}))w_1 + \mathbb{1}_G \bar{u} w_2, \\ f_2(x, \bar{u}, \underline{v}) - f_2(x, \bar{u}, \underline{v}) &= (m_{c_2} - \mathbb{1}_G(\underline{v} + \bar{v} + \bar{u}))w_2 + \mathbb{1}_G \bar{v} w_1. \end{aligned}$$

Inserting these into (3.2) yields

$$\begin{aligned}
 & \frac{1}{2} \frac{d}{dt} \int_{\Omega} \left[(w_1^+)^2 + (w_2^+)^2 \right] dx \\
 & \leq \int_{\Omega} (m_{c_1} - \mathbb{1}_G(\underline{u} + \bar{u} + \bar{v}))(w_1^+)^2 dx \\
 & \quad + \int_{\Omega} (m_{c_2} - \mathbb{1}_G(\underline{v} + \bar{v} + \bar{u}))(w_2^+)^2 dx \\
 & \quad + \int_{\Omega} (\bar{u}w_1^+w_2 + \bar{v}w_2^+w_1) dx \\
 & \leq \int_{\Omega} \left[(m_{c_1} - \mathbb{1}_G\underline{u})(w_1^+)^2 + (m_{c_2} - \mathbb{1}_G\underline{v})(w_2^+)^2 \right] dx + \int_{\Omega} (\bar{u} + \bar{v})w_1^+w_2^+ dx.
 \end{aligned}$$

Notice that in the second inequality, we have used that $\bar{u}, \bar{v} \geq 0$ so that $\bar{u}w_1^+w_2 = \bar{u}w_1^+(w_2^+ - w_2^-) \leq \bar{u}w_1^+w_2^+$. A similar inequality holds for $\bar{v}w_2^+w_1$.

Next, applying Young’s inequality to the mixed term yields

$$\begin{aligned}
 & \frac{1}{2} \frac{d}{dt} \int_{\Omega} \left[(w_1^+)^2 + (w_2^+)^2 \right] dx \\
 & \leq \int_{\Omega} (m_{c_1} - \mathbb{1}_G\underline{u} + (\bar{u} + \bar{v})/2)(w_1^+)^2 dx \\
 & \quad + \int_{\Omega} (m_{c_2} - \mathbb{1}_G\underline{v} + (\bar{u} + \bar{v})/2)(w_2^+)^2 dx \\
 & \leq \beta(t) \int_{\Omega} \left[(w_1^+)^2 + (w_2^+)^2 \right] dx,
 \end{aligned}$$

where the existence of such a function $\beta(t)$ again follows from the fact that all sub/super solution pairs belong to $C([0, T], C(\bar{\Omega}))$. Gronwall’s inequality then gives

$$\int_{\Omega} \left((w_1^+)^2 + (w_2^+)^2 \right) dx \leq e^{2 \int_0^t \beta(s) ds} \int_{\Omega} \left((w_1^+(0))^2 + (w_2^+(0))^2 \right) dx = 0,$$

since $w_1^+(0) = \max\{0, \underline{u}(x, 0) - \bar{u}(x, 0)\} = 0$ and $w_2^+(0) = \max\{0, \underline{v}(x, 0) - \bar{v}(x, 0)\} = 0$ by assumption. Consequently, $w_i^+ = 0$, and hence $w_i \leq 0$ a.e. in Q_T for each i , i.e. $\underline{u} \leq \bar{u}$ and $\underline{v} \leq \bar{v}$ a.e. in Q_T . Finally, by the Sobolev embedding all quantities are continuous in Q_T , and hence the inequality holds everywhere in Q_T . This completes the proof of the first part of the theorem.

(2) Next, notice the Sobolev embedding ensures that $\underline{u}, \bar{u}, \underline{v}, \bar{v} \in C^1(\bar{\Omega})$ for all $t \in (0, T)$. If in addition we assume that $\underline{u}, \bar{u}, \underline{v}, \bar{v} \in C^1((0, T); C(\bar{\Omega}))$, we may apply the strong maximum principle as follows. Since $w_1 \leq 0$, the hypothesis of (Arena 1972, Theorem 1) is satisfied. Suppose there exists a point $(x_0, t_0) \in \Omega \times (0, T)$ such that $z = 0$. Then, by (Arena 1972, Theorem 1), it must be the case that $w_1 \equiv 0$ in Ω for all $t \in (0, t_0)$. This contradicts the fact that $w_1(x, 0) = \underline{u}(x, 0) - \bar{u}(x, 0) < 0$ for some $x \in \Omega$. Hence, $w_1 < 0$ for all $(x, t) \in \Omega \times (0, T)$, i.e. $\underline{u} < \bar{u}$ for all $(x, t) \in \Omega \times (0, T)$.

As a final note, suppose that there exists $x_0 \in \partial\Omega$ such that $w_1(x_0, t_0) = 0$ for some $t_0 > 0$. Hopf’s lemma then guarantees that $\frac{\partial w_1}{\partial \mathbf{n}} > 0$, which is clearly in contradiction to the assumption that $\frac{\partial w_1}{\partial \mathbf{n}} = \frac{\partial u}{\partial \mathbf{n}} - \frac{\partial \bar{u}}{\partial \mathbf{n}} \leq 0$. Hence, $\underline{u} < \bar{u}$ for all $(x, t) \in \bar{\Omega} \times (0, T)$.

The same procedure yields that $\underline{v} < \bar{v}$ using instead that $\underline{u} \leq \bar{u}$ from (1) and the boundary conditions for \underline{v}, \bar{v} . This completes the proof of the second part, and concludes the proof of the theorem. \square

3.2 Well-posedness and strong monotonicity

In this section, we briefly discuss the well-posedness of problem (1.1), or more precisely, the existence and regularity of solutions, in addition to monotonicity properties of the induced semiflow. Usually, details of this nature are suppressed as they follow from classical results; however, due to the discontinuity of the heterogeneity in our system, some care must be given in order to determine the strong monotonicity of the system. We remind readers that $Q_T = \Omega \times (0, T)$.

Definition 3.1 A *strong solution* on $[0, T)$ to (1.1) a solution pair (u, v) which belongs to

$$\left[W_p^{2,1}(Q_T) \cap C([0, T); C(\bar{\Omega})) \right]^2$$

for any $p \geq 1$, satisfies the system almost everywhere in Ω and satisfies the boundary condition everywhere on $\partial\Omega$. A *global strong solution* is a strong solution on $[0, T)$ for all $T > 0$.

Definition 3.2 A *steady state* to (1.1) is a solution pair (\tilde{u}, \tilde{v}) which belongs to $[W^{2,p}(\Omega)]^2$ for any $p \geq 1$, satisfies the system almost everywhere in Ω and satisfies the boundary condition everywhere on $\partial\Omega$. A steady state (\tilde{u}, \tilde{v}) is referred to as a *coexistence steady state* if $(\tilde{u}, \tilde{v}) \in [C^+(\bar{\Omega}) \setminus \{0\}]^2$.

Theorem 3.1 For any initial data $(u_0, v_0) \in C^+(\bar{\Omega}) \times C^+(\bar{\Omega})$, there exists a unique global strong solution (u, v) to (1.1) satisfying $(u, v) \in [C^\alpha([0, \infty); C^+(\bar{\Omega})) \cap C^1((0, \infty); C^+(\bar{\Omega}))]^2$ for any $\alpha \in (0, 1)$. Moreover, solutions to problem (1.1) are strongly monotone in the sense that if $(u_0, v_0), (\tilde{u}_0, \tilde{v}_0) \in C^+(\bar{\Omega}) \times C^+(\bar{\Omega})$ are such that $(u_0, v_0) <_K (\tilde{u}_0, \tilde{v}_0)$, then $(u(\cdot, t), v(\cdot, t)) \ll_K (\tilde{u}(\cdot, t), \tilde{v}(\cdot, t))$ for all $t > 0$

Proof We may repeat the same process given in the scalar case in order to deduce some preliminary regularity results. That is, regularize all discontinuities and argue via compactness. Then, choose p large enough so that in fact $(u, v) \in [C^{1+\alpha, (1+\alpha)/2}(\bar{\Omega} \times [0, T))]^2$ for any $\alpha \in (0, 1)$ by the Sobolev embedding (see e.g. Wu et al. (2006), Theorem 1.4.1). We then easily verify that the boundary conditions are satisfied in the classical sense due to the regularity obtained via the Sobolev embedding.

Next, we show that solutions are positive and global. First, we assert that the solution (u, v) is nonnegative. To see this, note that the equation for each solution can be written as

$$u_t = d_1 \Delta u + uF_1(t),$$

$$v_t = d_2 \Delta v + v F_2(t),$$

where $F_i(t) = m_i - \mathbb{1}_G(u + v)$ are bounded by some nonnegative function $\beta(t)$ for any $T > 0$. Multiplying each equation by $u^- = \max\{0, -u\}$ and $v^- = \max\{0, -v\}$ respectively and integrating over Ω , we find that

$$\frac{1}{2} \frac{d}{dt} \int_{\Omega} \left[(u^-)^2 + (v^-)^2 \right] dx \leq \beta(t) \int_{\Omega} \left[(u^-)^2 + (v^-)^2 \right] dx.$$

The result then follows from Gronwall’s inequality and the fact that $u^-(\cdot, 0) = v^-(\cdot, 0) = 0$.

Next, if one considers the pair $(\bar{u}, \bar{v}) = (Me^{\gamma t} \psi_1, 0)$ where ψ_1 is the first eigenfunction solving (A.2) corresponding to $\mu_1(d_1, m_{c_1})$, it is easy to see that

$$\bar{u}_t - d \Delta \bar{u} \geq \bar{u}(m_{c_1} - \mathbb{1}_G(\bar{u} + \bar{v})),$$

so long as $\gamma \geq \mu_1(d_1, m_{c_1})$. Hence, u is exponentially bounded in time and thus necessarily exists globally. Furthermore, we see that $u(x, t) > 0$ in $\bar{\Omega}$ for all $t > 0$ so long as $u_0(x) = u(x, 0) > 0$ somewhere in Ω . A similar argument holds for $v(x, t)$ when one considers $(\underline{u}, \bar{v}) = (0, Me^{\gamma t} \psi_1)$ where ψ_1 corresponds to $\mu_1(d_2, m_{c_2})$ and γ is chosen such that $\gamma + \mu_1(d_2, m_{c_2}) \geq 0$.

We may now improve the regularity in the time variable for application in the following section. Most important in this argument is the Hölder continuity of the solution in the variable t . This allows us to apply (Stewart 1980, Theorem 3) once again: since $u_0 \in C(\Omega)$ and $(x, t) \mapsto u(x, t)[m_{c_1} - \mathbb{1}_G(u(x, t) + v(x, t))]$ is Hölder continuous with exponent α in the variable t , we may conclude that $\frac{\partial u}{\partial t}$ exists and is uniformly continuous on $(0, \infty)$. Similarly, we conclude that $\frac{\partial v}{\partial t}$ exists and is also uniformly continuous on $(0, \infty)$. Consequently, the unique strong solution (u, v) belongs to $[C^\alpha([0, \infty); C(\bar{\Omega})) \cap C^1((0, \infty); C(\bar{\Omega}))]^2$.

With the sufficient regularity obtained, Proposition 3.1 (2) immediately gives us the strong monotonicity of the system, completing the proof. □

The strong monotonicity allows us to use the following result (see e.g. Hess 1991, Proposition 9.1 and Theorem 9.2 and Zhao 2017, Theorem 2.4.1). This result is only necessary when applied to Theorem 1.1 (4), and hence, we assume that $\mu_1(d_i, m_{c_i}) < 0$ for $i = 1, 2$. This ensures that both u^* and v^* exist.

Proposition 3.2 *Let $d_1, d_2 > 0$ and $c_1, c_2 \geq 0$ be such that $\mu_1(d_i, m_{c_i}) < 0$ for $i = 1, 2$. Suppose that every coexistence steady state of (1.1), if exists, is asymptotically stable. Then one of the following alternatives holds.*

- (a) *There exists a unique coexistence steady state of (1.1) which is globally asymptotically stable.*
- (b) *System (1.1) has no coexistence steady state, and one of $(u^*, 0)$ or $(0, v^*)$ is globally asymptotically stable, while the other is unstable.*

We also have the following existence-comparison theorem for the elliptic system.

Proposition 3.3 *Suppose that $\underline{u}, \bar{u}, \underline{v}, \bar{v}$ belong to $W^{2,p}(\Omega)$ for any $p \geq 1$ and satisfy the conditions:*

$$\begin{aligned} -d_1 \Delta \underline{u} &\leq \underline{u}(m_{c_1} - \mathbb{1}_G(\underline{u} + \bar{v})) \quad \text{a.e. in } \Omega, \\ -d_2 \Delta \underline{v} &\leq \underline{v}(m_{c_2} - \mathbb{1}_G(\bar{u} + \underline{v})) \quad \text{a.e. in } \Omega, \\ -d_1 \Delta \bar{u} &\geq \bar{u}(m_{c_1} - \mathbb{1}_G(\bar{u} + \underline{v})) \quad \text{a.e. in } \Omega, \\ -d_2 \Delta \bar{v} &\geq \bar{v}(m_{c_2} - \mathbb{1}_G(\underline{u} + \bar{v})) \quad \text{a.e. in } \Omega, \\ \frac{\partial \underline{u}}{\partial \mathbf{n}} &\leq \frac{\partial \bar{u}}{\partial \mathbf{n}} \quad \text{on } \partial\Omega, \\ \frac{\partial \underline{v}}{\partial \mathbf{n}} &\leq \frac{\partial \bar{v}}{\partial \mathbf{n}} \quad \text{on } \partial\Omega. \end{aligned}$$

If $\underline{u}, \bar{u}, \underline{v}, \bar{v}$ satisfy $(\underline{u}, \bar{v}) \leq_K (\bar{u}, \underline{v})$, then

– there exist steady states $(\underline{u}^*, \bar{v}^*)$ and $(\bar{u}^*, \underline{v}^*)$ to (1.1) such that

$$(\underline{u}, \bar{v}) \leq_K (\underline{u}^*, \bar{v}^*) \leq_K (\bar{u}^*, \underline{v}^*) \leq_K (\bar{u}, \underline{v});$$

– any steady state (\hat{u}, \hat{v}) to (1.1) obeying $(\underline{u}, \bar{v}) \leq_K (\hat{u}, \hat{v}) \leq_K (\bar{u}, \underline{v})$ must satisfy

$$(\underline{u}^*, \bar{v}^*) \leq_K (\hat{u}, \hat{v}) \leq_K (\bar{u}^*, \underline{v}^*).$$

Proof The proof follows from standard iterative arguments and Aleksandrov’s maximum principle (see e.g. Gilbarg and Trudinger 1998, Chapter 9, Theorem 9.1) in place of the classical maximum principle. Some key details are provided here for completeness.

First, let K be so large that $F_1(x, u, v) := Ku + u(m_{c_1} - \mathbb{1}_G(u + v))$ and $F_2(x, u, v) := Kv + v(m_{c_2} - \mathbb{1}_G(u + v))$ are non-decreasing in the arguments u and v , respectively. We then iterate through the process

$$\begin{aligned} -d_1 u_k + K u_k &= F_1(x, u_{k-1}, v_{k-1}), \\ -d_2 v_k + K v_k &= F_2(x, u_{k-1}, v_{k-1}), \end{aligned}$$

subject to homogeneous Neumann boundary conditions. We then use $(\underline{u}, \bar{v}) = (\underline{u}_0, \bar{v}_0)$ and $(\bar{u}_0, \underline{v}_0)$ as initial iterates to create monotonic sequences satisfying

$$\underline{u} \leq \underline{u}_k \leq \underline{u}_{k+1} \leq \bar{u}_{k+1} \leq \bar{u}_k \leq \bar{u}, \quad \underline{v} \leq \underline{v}_k \leq \underline{v}_{k+1} \leq \bar{v}_{k+1} \leq \bar{v}_k \leq \bar{v},$$

for all $k \geq 1$. Interested readers are directed to (Pao 1992, Chapter 8.4) for further details.

Once these monotone sequences are constructed, the following pointwise limits exist

$$\lim_{k \rightarrow \infty} \underline{u}_k = \underline{u}^*, \quad \lim_{k \rightarrow \infty} \bar{u}_k = \bar{u}^*, \quad \lim_{k \rightarrow \infty} \underline{v}_k = \underline{v}^*, \quad \lim_{k \rightarrow \infty} \bar{v}_k = \bar{v}^*,$$

with convergence understood in the sense of $W^{2,p}(\Omega)$ for any $p \geq 1$. Since each $F_i(x, u, v)$ are Lipschitz continuous in the arguments u, v , one may then apply standard L^p theory of elliptic equations in order to deduce that these limit functions are indeed solutions to the steady state problem associated with (1.1). By the Sobolev embedding we have that in fact all solutions belong to $C^1(\bar{\Omega})$, and so also satisfy the boundary conditions everywhere on $\partial\Omega$ in the classical sense. The ordering relation of these solution obtained then follows immediately due to the ordering of the original sequences.

Finally, if (u^*, v^*) is any other solution lying between the original sub/super solutions pairs, choosing $(u_0, \bar{v}_0) = (u^*, v^*)$ yields $\underline{u}^* \leq u^*$ and $\bar{v}^* \geq v^*$. A similar argument yields $\bar{u}^* \geq u^*$ and $\underline{v}^* \leq v^*$, completing the proof. \square

We conclude this subsection with the following simple result.

Corollary 3.2 *If a coexistence steady state (\tilde{u}, \tilde{v}) to (1.1) exists, there must hold $(\tilde{u}, \tilde{v}) \in C^{++}(\Omega) \times C^{++}(\Omega)$.*

Proof It is easy to see that $(0, v^*) \leq_K (\tilde{u}, \tilde{v}) \leq_K (u^*, 0)$ from Proposition 3.3. The result then follows from of Proposition 3.1 (2) with $(\underline{u}, \bar{v}) = (0, v^*)$ and $(\bar{u}, \underline{v}) = (u^*, 0)$. \square

3.3 Global dynamics and proof of main results

We prove Theorems 1.1 and 1.3 in this section. For notational simplicity, we omit Neumann boundary conditions whenever no confusion is caused.

Proof of Theorem 1.1 (1)-(3) Parts (1)–(3) follow from standard arguments. We include the proofs for completeness. Denote by (u, v) the unique global strong solution to (1.1) with initial data $(u_0, v_0) \in [C^+(\bar{\Omega}) \setminus \{0\}]^2$.

(1) Suppose $\mu_1(d_i, m_{c_i}) > 0$ for $i = 1, 2$. Define $(\underline{u}, \bar{v}) := (0, w_2)$ and $(\bar{u}, \underline{v}) := (w_1, 0)$ in $\bar{\Omega} \times [0, \infty)$, where w_1 and w_2 are respectively solutions to (1.3) with $(d, m) = (d_1, m_{c_1})$ and $(d, m) = (d_2, m_{c_2})$ subject to the initial conditions $w_1(\cdot, 0) = u_0$ and $w_2(\cdot, 0) = v_0$. By Theorem 2.2, $w_i(\cdot, t) \rightarrow 0$ in $C(\bar{\Omega})$ as $t \rightarrow \infty$ for $i = 1, 2$.

Direct computation shows that the differential inequalities in Proposition 3.1 hold, that is, (\underline{u}, \bar{v}) and (\bar{u}, \underline{v}) are respectively a sub solution and a super solution of (1.1). We conclude from Proposition 3.1 that $0 \leq u \leq \bar{u}$ and $0 \leq v \leq \bar{v}$ in $\bar{\Omega}$ for all $t > 0$. Hence, $(u, v) \rightarrow (0, 0)$ in $C(\bar{\Omega}) \times C(\bar{\Omega})$ as $t \rightarrow \infty$, completing the proof.

Next we prove the result for case (3). Case (2) follows in a similar fashion. Suppose that $\mu_1(d_1, m_{c_1}) \geq 0$ and that $\mu_1(d_2, m_{c_2}) < 0$ so that v^* exists.

Let w be the unique solution of (1.3) with $(d, m) = (d_1, m_{c_1})$ and initial data $w_0 = u_0$. Theorem 2.2 (ii) ensures that $w \rightarrow 0$ in $C(\bar{\Omega})$ as $t \rightarrow \infty$. Obviously, w satisfies

$$w_t - d_1 \Delta w \geq w(m_{c_1} - \mathbb{1}_G(w + v)) \quad \text{a.e. in } \Omega \times (0, \infty),$$

and hence, $u \leq w$ by Proposition 2.1. It follows that $u \rightarrow 0$ in $C(\bar{\Omega})$ as $t \rightarrow \infty$, and thus, for any $0 < \varepsilon \ll 1$, there is $t_\varepsilon \gg 1$ such that $0 \leq u \leq \varepsilon$ in $\bar{\Omega}$ for all $t \geq t_\varepsilon$. Let z_ε be the strong solution to the following auxiliary problem

$$\begin{cases} z_t = d_2 \Delta z + z(m_{c_2} - \mathbb{1}_G(z + \varepsilon)) & \text{in } \Omega \times (t_\varepsilon, \infty), \\ z(\cdot, t_\varepsilon) = v(\cdot, t_\varepsilon) & \text{in } \overline{\Omega}. \end{cases}$$

Proposition 2.1 yields that $z_\varepsilon \leq v$ for all $t \geq t_\varepsilon$.

Recall that $\mu_1(d_2, m_{c_2}) < 0$ by assumption. By Proposition A.2 (iii), we may choose ε so small that $\mu_1(d_2, m_{c_2} - \varepsilon \mathbb{1}_G) < 0$. Then, the following equation:

$$d_2 \Delta z^* + z^*(m_{c_2} - \mathbb{1}_G(z^* + \varepsilon)) = 0 \quad \text{in } \Omega$$

admits a unique positive solution z_ε^* . It follows from Theorem 2.2 that $z_\varepsilon \rightarrow z_\varepsilon^*$ in $C(\overline{\Omega})$ as $t \rightarrow \infty$.

Finally, let \bar{v} solve

$$\begin{cases} \bar{v}_t = d_2 \Delta \bar{v} + \bar{v}(m_{c_2} - \mathbb{1}_G \bar{v}) & \text{in } \Omega \times (0, \infty), \\ \bar{v}(\cdot, 0) = v_0 & \text{in } \overline{\Omega}. \end{cases}$$

By Theorem 2.2, $\bar{v} \rightarrow v^*$ as $t \rightarrow \infty$. Note that by Proposition 2.1, $v \leq \bar{v}$ in $\overline{\Omega}$ for all $t > 0$. Combining these results, we deduce that

$$z_\varepsilon^* = \lim_{t \rightarrow \infty} z_\varepsilon \leq \liminf_{t \rightarrow \infty} v \leq \limsup_{t \rightarrow \infty} v \leq \lim_{t \rightarrow \infty} \bar{v} = v^*, \quad \forall 0 < \varepsilon \ll 1.$$

We conclude by showing that $z_\varepsilon^* \rightarrow v^*$ in $C(\overline{\Omega})$ as $\varepsilon \rightarrow 0$. It is clear that the family $\{z_\varepsilon^*\}_\varepsilon$ is uniformly bounded in $L^\infty(\Omega)$, and hence is uniformly bounded in $L^p(\Omega)$ for any $p \geq 1$. Consequently, standard elliptic L^p -estimates (see e.g. Wu et al. 2006, chapter 9) imply that $\{z_\varepsilon^*\}_\varepsilon$ is uniformly bounded in $W^{2,p}(\Omega)$, and by compactness, there exists a subsequence, still denoted by $\{z_\varepsilon^*\}_\varepsilon$, such that $z_\varepsilon^* \rightarrow z_0^*$ in $L^p(\Omega)$ as $\varepsilon \rightarrow 0$. Hence, $z_\varepsilon^*(m_{c_2} - \varepsilon \mathbb{1}_G - \mathbb{1}_G z_\varepsilon^*) \rightarrow z_0^*(m_{c_2} - \mathbb{1}_G z_0^*)$ in $L^p(\Omega)$ as $\varepsilon \rightarrow 0$. In particular, this means that $\{z_\varepsilon^*\}_\varepsilon$ is a Cauchy sequence in $L^p(\Omega)$. Then, by the same L^p -estimates, we see that $\{z_\varepsilon^*\}_\varepsilon$ is a Cauchy sequence in $W^{2,p}(\Omega)$. Since $W^{2,p}(\Omega)$ is a Banach space, there exists a unique limit denoted by z_0^* such that $z_\varepsilon \rightarrow z_0^*$ in $W^{2,p}(\Omega)$ as $\varepsilon \rightarrow 0$. We now see that z_0^* must satisfy $-d_2 \Delta z_0^* = \mathbb{1}_G z_0^*(1 - z_0^*)$ a.e. in Ω . Furthermore, the convergence in $W^{2,p}(\Omega)$ for p sufficiently large implies the convergence in $C^1(\overline{\Omega})$, and so z_0^* satisfies $\frac{\partial z_0^*}{\partial n} = 0$ on $\partial\Omega$. It follows that z_0^* is a strong solution satisfying the same equation as v^* . The uniqueness of solutions implies that $z_0^* = v^*$ in $\overline{\Omega}$. This completes the proof. \square

The rest of this section is devoted to the proof of Theorem 1.1 (4) with the short proof of Theorem 1.3 presented at the end of this section.

In the next two results, we study the local stability of semi-trivial steady states of (1.1). Whenever $\mu_1(d_1, m_{c_1}) < 0$ (resp. $\mu_1(d_2, m_{c_2}) < 0$), we denote by u^* (resp. v^*) the unique positive steady state of (1.3) with $(d, c) = (d_1, c_1)$ (resp. $(d, c) = (d_2, c_2)$). Therefore, Lemma 2.4 applies to u^* and v^* with respect to c_1 and c_2 , respectively.

Lemma 3.3 *Suppose $c_1 > 0$ and $\mu_1(d_1, m_{c_1}) < 0$. Then there exists a critical value $\bar{c}_2^* \in (0, c_1)$ such that the following hold:*

- (i) If $c_2 \in (0, \bar{c}_2^*)$, then $(u^*, 0)$ is unstable;
- (ii) If $c_2 \in (\bar{c}_2^*, c_1)$, then $(u^*, 0)$ is linearly stable.

Furthermore, \bar{c}_2^* satisfies $\bar{c}_2^* > \bar{c}_2 := \frac{|G| - \int_G u^*}{|B|} > 0$.

Proof Consider the following eigenvalue problem associated to the linearization of (1.1) about $(u^*, 0)$:

$$\begin{cases} d_1 \Delta \psi_1 + (m_{c_1} - 2\mathbb{1}_G u^*)\psi_1 - \mathbb{1}_G u^* \psi_2 + \lambda \psi_1 = 0 & \text{in } \Omega, \\ d_2 \Delta \psi_2 + (m_{c_2} - \mathbb{1}_G u^*)\psi_2 + \lambda \psi_2 = 0 & \text{in } \Omega. \end{cases} \tag{3.3}$$

In particular,

$$d_2 \Delta \psi_2 + (m_{c_2} - \mathbb{1}_G u^*)\psi_2 + \lambda \psi_2 = 0 \quad \text{in } \Omega, \tag{3.4}$$

and so all eigenvalues are real.

Since $|G| > \int_G u^*$ due to Lemma 2.4, we deduce $\int_\Omega (m_{c_2} - \mathbb{1}_G u^*) = |G| - \int_G u^* - c_2 |B| \geq 0$ for all $c_2 \leq \bar{c}_2$, where \bar{c}_2 is as in the statement. It follows from Proposition A.2 that

$$\mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*) < 0, \quad \forall c_2 \leq \bar{c}_2, \tag{3.5}$$

where $\mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*)$ is the first eigenvalue of (3.4).

Assume $c_2 \leq \bar{c}_2$ and let ψ_2 be the positive eigenfunction associated to $\lambda := \mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*) < 0$. We solve for ψ_1 in the first equation of (3.3) given by

$$d_1 \Delta \psi_1 + (m_{c_1} - 2\mathbb{1}_G u^*)\psi_1 - \mathbb{1}_G u^* \psi_2 + \lambda \psi_1 = 0 \quad \text{in } \Omega. \tag{3.6}$$

Since $\mu_1(d_1, m_{c_1} - 2\mathbb{1}_G u^*) > \mu_1(d_1, m_{c_1} - \mathbb{1}_G u^*) = 0$ and $\lambda < 0$, the operator given by

$$d_1 \Delta + (m_{c_1} - 2\mathbb{1}_G u^*) + \lambda : C(\bar{\Omega}) \rightarrow C(\bar{\Omega}), \tag{3.7}$$

is invertible. This together with the Krein-Rutman theorem (see e.g. Hess 1991, Theorem 7.3) implies that (3.6) admits a unique positive solution. Hence, λ is a negative eigenvalue to the problem (3.3) and $(u^*, 0)$ is unstable.

So far, we have shown that $(u^*, 0)$ is unstable for $c_2 \in (0, \bar{c}_2]$. We extend this interval to $(0, \bar{c}_2^*)$ for some $\bar{c}_2^* > \bar{c}_2$. First, if we choose $c_2 = c_1$ so that $m_{c_2} = m_{c_1}$, we see from Proposition A.2 (iii) that $\mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*) > \mu_1(d_1, m_{c_2} - \mathbb{1}_G u^*) = 0$. This together with (3.5) and the monotonicity of $c_2 \mapsto \mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*)$ yields the existence of a unique value $\bar{c}_2^* \in (\bar{c}_2, c_1)$ such that $\mu_1(d_2, m_{\bar{c}_2^*} - \mathbb{1}_G u^*) = 0$. In particular, $\mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*) < 0$ for all $c_2 \in (0, \bar{c}_2^*)$. Hence, the operator (3.7) is again invertible for all $c_2 \in (0, \bar{c}_2^*)$ and so $(u^*, 0)$ is unstable. This proves part (i) of the proposition.

It remains to show that $(u^*, 0)$ is linearly stable for all $c_2 \in (\bar{c}_2^*, c_1)$. Referring back to the eigenvalue problem (3.3), if $\psi_2 \not\equiv 0$, then λ must satisfy $\lambda \geq \mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*) > 0$, as $c_2 \in (\bar{c}_2^*, c_1)$. On the other hand, if $\psi_2 \equiv 0$, one considers only

$$d_1 \Delta \psi_1 + (m_{c_1} - 2\mathbb{1}_G u^*)\psi_1 + \lambda \psi_1 = 0 \quad \text{in } \Omega,$$

and notices that $\lambda \geq \mu_1(d_1, m_{c_1} - 2\mathbb{1}_G u^*) > \mu_1(d_1, m_{c_1} - \mathbb{1}_G u^*) = 0$. In either case, all eigenvalues of (3.3) are positive, and thus, $(u^*, 0)$ is linearly stable for all $c_2 \in (\bar{c}_2^*, c_1)$. This completes the proof of part (ii). \square

Lemma 3.4 *Let $c_1 > 0$ and $\mu_1(d_2, m_{c_2}) < 0$. There exists a critical value $\underline{c}_2^* \in (0, c_1)$ such that the following hold:*

- (i) *If $c_2 \in (0, \underline{c}_2^*)$, then $(0, v^*)$ is linearly stable;*
- (ii) *If $c_2 \in (\underline{c}_2^*, c_1)$, then $(0, v^*)$ is unstable.*

Furthermore, \underline{c}_2^* satisfies $\underline{c}_2^* > \underline{c}_2 := \sup \{c_2 > 0 : v^* \geq u^* \text{ in } G\} > 0$.

Proof Consider the following eigenvalue problem associated to the linearization of (1.1) about $(0, v^*)$:

$$\begin{cases} d_1 \Delta \psi_1 + (m_{c_1} - \mathbb{1}_G v^*)\psi_1 + \lambda \psi_1 = 0 & \text{in } \Omega, \\ d_2 \Delta \psi_2 + (m_{c_2} - 2\mathbb{1}_G v^*)\psi_2 - \mathbb{1}_G v^* \psi_1 + \lambda \psi_2 = 0 & \text{in } \Omega. \end{cases} \quad (3.8)$$

By Lemma 2.4, $u^* < 1$ in $\bar{\Omega}$, and $v^* \rightarrow 1$ in $C(\bar{\Omega})$ as $c_2 \rightarrow 0$, and thus, $u^* \leq v^*$ in G if c_2 is sufficiently small. Hence, \underline{c}_2 is well-defined. Proposition A.2 (iv) yields that

$$\mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*) > \mu_1(d_1, m_{c_1} - \mathbb{1}_G u^*) = 0, \quad \forall c_2 \in (0, \underline{c}_2).$$

If $\psi_1 \not\equiv 0$, then $\lambda \geq \mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*) > 0$. If $\psi_1 \equiv 0$, then $\lambda \geq \mu_1(d_2, m_{c_2} - 2\mathbb{1}_G v^*) > \mu_1(d_2, m_{c_2} - \mathbb{1}_G v^*) = 0$. In either case, all eigenvalues of (3.8) are positive for $c_2 \in (0, \underline{c}_2)$, and so $(0, v^*)$ is linearly stable for $c_2 \in (0, \underline{c}_2)$.

We now extend the interval $(0, \underline{c}_2)$ to $(0, \underline{c}_2^*)$. Notice that if we choose $c_2 = c_1$, then

$$\mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*) = \mu_1(d_1, m_{c_2} - \mathbb{1}_G v^*) < \mu_1(d_2, m_{c_2} - \mathbb{1}_G v^*) = 0,$$

and hence there exists a critical value $\underline{c}_2^* > \underline{c}_2$ such that $\mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*) = 0$. Consequently, $(0, v^*)$ is linearly stable for all $c_2 \in [0, \underline{c}_2^*)$.

Finally, we show that $(0, v^*)$ is unstable for all $c_2 \in \underline{c}_2^*$. Referring back to the linearized system (3.8), set $\lambda = \mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*) < 0$ and denote by ψ_1 the corresponding eigenfunction. We now solve for ψ_2 . This follows immediately from the fact that the operator $d_2 \Delta + (m_{c_2} - 2\mathbb{1}_G v^*) + \lambda$ is invertible since $\mu_1(d_2, m_{c_2} - 2\mathbb{1}_G v^*) > 0$ and $\lambda < 0$. Hence, (3.8) has a negative eigenvalue for all $c_2 > \underline{c}_2^*$ and so $(0, v^*)$ is unstable. This completes the proof. \square

Next, we state a result asserting that every coexistence steady state is linearly stable, whenever it exists. This key result in conjunction with Proposition 3.2 will allow us to prove the subsequent Lemma, which results in conclusions of global asymptotic stability.

Lemma 3.5 *Suppose $0 < d_1 < d_2$ and $0 \leq c_2 < c_1$. Then, any coexistence steady state of (1.1), whenever it exists, is linearly stable.*

Proof We adapt the proof of (He and Ni 2015, claim (S)). Let (\tilde{u}, \tilde{v}) be a coexistence steady state of (1.1). Then, $(0, \tilde{v}) \ll_K (\tilde{u}, 0)$ by Corollary 3.2. Consider the eigenvalue problem associated to the linearization of (1.1) about (\tilde{u}, \tilde{v}) :

$$\begin{cases} d_1 \Delta \psi_1 + (m_{c_1} - \mathbb{1}_G(\tilde{u} + \tilde{v}) - \mathbb{1}_G \tilde{u})\psi_1 - \mathbb{1}_G \tilde{u} \psi_2 + \lambda \psi_1 = 0 & \text{in } \Omega, \\ d_2 \Delta \psi_2 + (m_{c_2} - \mathbb{1}_G(\tilde{u} + \tilde{v}) - \mathbb{1}_G \tilde{v})\psi_2 - \mathbb{1}_G \tilde{v} \psi_1 + \lambda \psi_2 = 0 & \text{in } \Omega. \end{cases} \quad (3.9)$$

Denote by (ϕ_1, ϕ_2) the eigenfunction pair associated to the principal eigenvalue λ_1 , whose existence and simplicity is ensured by the Krein-Rutman theorem. We may choose ϕ_1, ϕ_2 such that $(0, 0) \ll_K (\phi_1, \phi_2)$ and $\|\phi_1\|_2^2 + \|\phi_2\|_2^2 = 1$. Here, the ordering of ϕ_1, ϕ_2 is a consequence of the existence of the eigenfunction pair obtained in the ordered cone $(X) \times (-X)$, where $X = C^{++}(\bar{\Omega})$. Direct calculations give

$$d_1 \nabla \cdot \left(\tilde{u}^2 \nabla \left(\frac{\phi_1}{\tilde{u}} \right) \right) = \mathbb{1}_G \tilde{u}^2 (\phi_1 + \phi_2) - \lambda_1 \tilde{u} \phi_1 \quad \text{in } \Omega.$$

Multiplying the above identity by $\frac{\phi_1^2}{\tilde{u}^2}$ and integrating over Ω , we find

$$-2d_1 \int_{\Omega} \tilde{u} \phi_1 \left| \nabla \left(\frac{\phi_1}{\tilde{u}} \right) \right|^2 dx = \int_G \phi_1^2 (\phi_1 + \phi_2) dx - \lambda_1 \int_{\Omega} \frac{\phi_1^3}{\tilde{u}} dx.$$

Similarly, there holds

$$-2d_2 \int_{\Omega} \tilde{v} \phi_2 \left| \nabla \left(\frac{\phi_2}{\tilde{v}} \right) \right|^2 dx = \int_G \phi_2^2 (\phi_1 + \phi_2) dx - \lambda_1 \int_{\Omega} \frac{\phi_2^3}{\tilde{v}} dx.$$

Combining these two identities, we find

$$\begin{aligned} -\lambda_1 \int_{\Omega} \left(\frac{\phi_1^3}{\tilde{u}} - \frac{\phi_2^3}{\tilde{v}} \right) dx &= -2d_1 \int_{\Omega} \tilde{u} \phi_1 \left| \nabla \left(\frac{\phi_1}{\tilde{u}} \right) \right|^2 dx - \int_G \phi_1^2 (\phi_1 + \phi_2) dx \\ &\quad + 2d_2 \int_{\Omega} \tilde{v} \phi_2 \left| \nabla \left(\frac{\phi_2}{\tilde{v}} \right) \right|^2 dx + \int_G \phi_2^2 (\phi_1 + \phi_2) dx \\ &\leq - \int_G (\phi_1 + \phi_2) (\phi_1^2 - \phi_2^2) dx \\ &= - \int_G (\phi_1 + \phi_2)^2 (\phi_1 - \phi_2) dx \leq 0. \end{aligned}$$

This implies that $\lambda_1 \geq 0$ with equality if and only if $\frac{\phi_1}{u} \equiv \text{const}$, $\frac{\phi_2}{v} \equiv \text{const}$ and $\phi_1 = -\phi_2$.

If (\tilde{u}, \tilde{v}) is not linearly stable, then $\lambda_1 = 0$. It follows that $\tilde{u} = k\tilde{v}$ for some $k > 0$, which together with the system satisfied by (\tilde{u}, \tilde{v}) gives

$$\begin{cases} d_1 \Delta \tilde{u} + \tilde{u}(m_{c_1} - \mathbb{1}_G(1 + k^{-1})\tilde{u}) = 0 & \text{in } \Omega, \\ d_2 \Delta \tilde{v} + \tilde{v}(m_{c_2} - \mathbb{1}_G(1 + k)\tilde{v}) = 0 & \text{in } \Omega. \end{cases}$$

Clearly, $w^* := (1 + k^{-1})\tilde{u} = (1 + k)\tilde{v}$ satisfies

$$\begin{cases} d_1 \Delta w^* + w^*(m_{c_1} - \mathbb{1}_G w^*) = 0 & \text{in } \Omega, \\ d_2 \Delta w^* + w^*(m_{c_2} - \mathbb{1}_G w^*) = 0 & \text{in } \Omega. \end{cases}$$

Hence, w^* satisfies $(d_2 - d_1) \Delta w^* - \mathbb{1}_B(c_1 - c_2)w^* = 0$ in Ω , leading to $w^* = 0$ in Ω . This contradicts the positivity of \tilde{u} and \tilde{v} . In conclusion, $\lambda_1 > 0$, and hence, (\tilde{u}, \tilde{v}) is linearly stable. □

Lemma 3.5 allows us to show an additional property of the quantities \underline{c}_2^* and \bar{c}_2^* .

Lemma 3.6 *It holds $\underline{c}_2^* < \bar{c}_2^*$. Moreover;*

- (i) *If $c_2 \in [0, \underline{c}_2^*) \cup (\bar{c}_2^*, \infty)$, there is no coexistence steady state;*
- (ii) *If $c_2 \in (\underline{c}_2^*, \bar{c}_2^*)$, then there exists a unique coexistence steady state.*

Proof First, we claim that $\underline{c}_2^* < \bar{c}_2^*$. Suppose otherwise. We then consider two cases: $\underline{c}_2^* > \bar{c}_2^*$ and $\underline{c}_2^* = \bar{c}_2^*$.

In the first case, whenever $c_2 \in (\bar{c}_2^*, \underline{c}_2^*)$, both $(u^*, 0)$ and $(0, v^*)$ are linearly stable according to Lemmas 3.3 and 3.4. Such a case is contradictory to Proposition 3.2.

Suppose now that $\underline{c}_2^* = \bar{c}_2^*$. Let c_2 be exactly this value. Note that v^* is fixed corresponding to c_2 , whereas u^* is fixed and independent of c_2 . From the definition of \underline{c}_2^* and \bar{c}_2^* , we find simultaneously that

$$\mu_1(d_1, m_{c_1} - \mathbb{1}_G v^*) = 0 = \mu_1(d_2, m_{c_2} - \mathbb{1}_G u^*)$$

for some eigenfunctions ψ_1, ψ_2 , while $0 = \mu_1(d_1, m_{c_1} - \mathbb{1}_G u^*) = \mu_1(d_2, m_{c_2} - \mathbb{1}_G v^*)$ with eigenfunctions u^* and v^* , respectively. In other words, the following equations are satisfied:

$$\begin{aligned} d_1 \Delta \psi_1 + (m_{c_1} - \mathbb{1}_G v^*)\psi_1 &= 0, & d_1 \Delta u^* + u^*(m_{c_1} - \mathbb{1}_G u^*) &= 0, \\ d_2 \Delta \psi_2 + (m_{c_2} - \mathbb{1}_G u^*)\psi_2 &= 0, & d_2 \Delta v^* + v^*(m_{c_2} - \mathbb{1}_G v^*) &= 0, \end{aligned}$$

From the variational characterization of these eigenvalues, we have that

$$0 \leq \int_{\Omega} \left[d_2 |\nabla \phi|^2 - \phi^2(m_{c_2} - \mathbb{1}_G u^*) \right] dx, \quad \forall \phi \in H^1(\Omega) : \phi \not\equiv 0,$$

$$0 = \int_{\Omega} \left[d_2 |\nabla v^*|^2 - (v^*)^2 (m_{c_2} - \mathbb{1}_G v^*) \right] dx, \tag{3.10}$$

and also

$$\begin{aligned} 0 &\leq \int_{\Omega} \left[d_1 |\nabla \phi|^2 - \phi^2 (m_{c_1} - \mathbb{1}_G v^*) \right] dx, \quad \forall \phi \in H^1(\Omega) : \phi \not\equiv 0, \\ 0 &= \int_{\Omega} \left[d_1 |\nabla u^*|^2 - (u^*)^2 (m_{c_2} - \mathbb{1}_G u^*) \right] dx. \end{aligned} \tag{3.11}$$

Note that the inequalities above are strict when ϕ is any function other than the principal eigenfunction. Hence, if we choose $\phi = v^*$ in the first equation appearing in (3.10) and take the difference of the two, we find that $\int_G (v^*)^2 (u^* - v^*) > 0$. Similarly, if we choose $\phi = u^*$ in the first equation appearing in (3.11) and take the difference of the two, we obtain $\int_G (u^*)^2 (v^* - u^*) > 0$. Adding these two quantities, we find

$$0 < \int_G (v^*)^2 (u^* - v^*) dx + \int_G (u^*)^2 (v^* - u^*) dx = - \int_G (u^* - v^*)^2 (u^* + v^*) dx \leq 0,$$

which is a contradiction. Hence, $c_2^* \neq \bar{c}_2^*$, and so combining these two cases implies that $c_2^* < \bar{c}_2^*$ must hold.

(i) Let $0 \leq c_2 < c_2^*$. Suppose on the contrary that there exists a coexistence steady state (\tilde{u}, \tilde{v}) . In this case, $(0, v^*)$ is linearly stable by Lemma 3.4, while (\tilde{u}, \tilde{v}) is globally asymptotically stable by Lemma 3.5 and Proposition 3.2, leading to a contradiction.

A similar argument holds when $c_2 > \bar{c}_2^*$.

(ii) Suppose $c_2 \in (c_2^*, \bar{c}_2^*)$. Then, both $(u^*, 0)$ and $(0, v^*)$ are unstable, and hence, Proposition 3.2 ensures the existence of a unique coexistence steady state. This completes the proof. \square

We are ready to prove Theorem 1.1 (4).

Proof of Theorem 1.1 (4) By Lemmas 3.3, 3.4 and 3.6, there holds $c_2^* < \bar{c}_2^* < c_1$.

(i) Suppose $c_2 \in (\bar{c}_2^*, c_1)$. By Lemma 3.3, $(u^*, 0)$ is linearly stable. Since $c_2 > c_2^*$, Lemma 3.4 implies that $(0, v^*)$ is unstable. By Lemma 3.6, there is no coexistence steady state. From Proposition 3.2, we conclude that $(u^*, 0)$ is globally asymptotically stable.

(ii) Suppose $c_2 \in (c_2^*, \bar{c}_2^*)$. Then, both $(u^*, 0)$ and $(0, v^*)$ are unstable. By Lemma 3.6, there exists a unique coexistence steady state, and is hence globally asymptotically stable by Proposition 3.2.

(iii) Suppose $c_2 \in (0, c_2^*)$. Then, $(0, v^*)$ is linearly stable by Lemma 3.4. By Lemma 3.3, $(u^*, 0)$ is unstable, and by Lemma 3.6, there is no coexistence steady state. Hence, Proposition 3.2 implies that $(0, v^*)$ is globally asymptotically stable. \square

Theorem 1.3 follows almost immediately from the previous results.

Proof of Theorem 1.3 It is easy to see that when $c_2 = 0 < c_1$, $(u^*, 0)$ is unstable while $(0, v^*)$ is linearly stable. From Lemma 3.6, we see that there cannot exist a coexistence steady state when $c_2 = 0$. Hence, $(0, v^*)$ is globally asymptotically stable by Proposition 3.2. \square

4 Discussion

In this paper we introduced a spatially explicit, two species competition-diffusion model in the presence of habitat degradation. The entire habitat Ω was broken into two distinct habitat types G and B . In the healthy region G , dynamics are governed by standard Lotka-Volterra competition, while in the degraded region B , both species decay exponentially (not necessarily at the same rate) without growth or competition. The asymptotic behaviour of solutions was rigorously investigated depending on the level of detriment experienced by each species in the degraded region, described by the parameters c_i , $i = 1, 2$. As suggested in the derivation, such a setup may be more or less reasonable depending on the interpretation for application purposes. In the case of interference competition (i.e. competition which occurs directly between individuals), the species may still interact within a degraded area of habitat. This could be derived through direct acts of aggression in order to prevent other individuals (within the same species) from accessing their mating partner. In this case, the intraspecific competition might be considered independent of habitat quality, and so assumption (iii) introduced in Sect. 1.2 may not be reasonable. In the scalar case, one could modify the reaction term to the form $u(m_c - u)$ (with a similar adjustment in the system case) in order to include the competition interaction in the degraded region B . However, the steady state in the limiting case $c = 0$ is no longer constant and will complicate the subsequent analysis to some degree. Nevertheless, it is worth noting that this says something interesting about the nature of the competition: under exploitative competition, the species will reach carrying capacity everywhere so long as the region G has positive area; in contrast, interference competition will result in a total population density strictly less than the carrying capacity, dependent on the size and shape of the favourable region G .

Through the application of classical PDE theory, some lesser known generalizations, and the theory of monotone flows, the global asymptotic stability of steady states was determined. Consistent with the classic result “the slower diffuser always wins” (Dockery et al. 1998), it was found that when the slower diffuser is also the stronger competitor, it will surely drive the weaker species to extinction. However, it was also found that if one species is particularly resilient to effects of the degraded region while the other species is affected more negatively, the resilient species will always drive the other to extinction! This result is best highlighted by the limiting case when $c_2 = 0 < c_1$. In this case, species u experiences *some* level of detriment in the degraded region while the impact on species v is completely neutral, and hence species v is found to always drive species u to extinction! The remarkable feature about this result is that it is independent of the size of the region B and the level of impact experienced in region B (given by c_1). That is to say, if there is no net growth or death of species v in the degraded region, as long as there is some amount of degraded habitat where species u experiences some level of detriment, species u always goes extinct. This outcome is consistent with the competitive exclusion principle, where even the slightest advantage over another species results in the persistence of the superior and extinction of the inferior species. On the other hand, in the case where both species experience some level of detriment in the degraded region, *coexistence is always a possibility*. This result aligns with what we see in reality, where competing species

occupying a similar ecological niche can sometimes coexist. In the end, this is a much more intuitive result than “the slower diffuser always wins”: the slower diffuser may or may not win, but the stronger competitor, where strength is measured in terms of resilience to the effects of degraded habitat, is given the competitive advantage. Such an outcome is at odds with more classical work, such as (Tilman et al. 1994), which predicts that the strongest or most superior competitor will always go extinct first. In this sense our results may be more realistic as they include the possibility to reverse the order of extinction. Indeed, it has been previously noted that extinction ordering does not necessarily proceed from best to worst, as the order depends on many other factors not included in Tilman’s original model (Lin and Liu 2006).

These results have obvious implications to conservation biology. As an example, one may consider a scenario in which two competing species occupy a conserved area of habitat. If the first species is particularly resilient to changes in local habitat quality, such as some rat species, even a slight decrease in quality of habitat for the second species could result in its local extinction. Consequently, care should be taken when implementing well intended conservation efforts, as unintended consequences due to counter-intuitive species interactions may play an important in species survival.

An additional feature of this model not fully investigated in the current work is that the model allows one to distinguish between habitat loss and the process of habitat fragmentation (i.e. habitat fragmentation *per se* (Fahrig 2003; Jackson and Fahrig 2013)). For example, if one holds the area of conserved habitat fixed, one may investigate the impacts of fragmentation (in the sense of variable configurations) through consideration of changes in stability based on configuration alone. In mathematical terms, one can discuss the effect of fragmentation through changes in the size and sign of the eigenvalue $\mu_1(d, m)$ when the area of the degraded region B is held fixed. Roughly speaking, all of the information concerning fragmentation is hidden within the properties of this eigenvalue, which clearly depends on geometric properties of the sets G and B . It is interesting to note that some results (see e.g. Cantrell and Cosner (1989), Theorem 3.1) indicate that a process of increasing fragmentation alone may result in assured deterministic extinction, while the amount of degradation in a particular region alone is not enough to guarantee extinction. A more precise investigation of these effects is currently in progress through consideration of the limiting case $\lim_{c \rightarrow \infty} \mu_1(d, m_c)$. A combination of such results may have strong implications towards the debate of fragmentation versus habitat loss and which process (independent of the other) is “worse” in terms of the survival of local populations. Furthermore, such a limiting case will provide deeper connections between the impacts of mere degradation compared to outright destruction.

In relation to the discussion above, as described in (Kun et al. 2019), we have a growing understanding of the various phases that altered land may go through. This includes the processes of habitat degradation, and habitat fragmentation. Although a detailed general analytic investigation of the eigenvalue problems discussed here is unrealistic, simulations provide an avenue of investigation to more accurately determine the impact of these changes in environment on the local species. Most importantly, it is understood that the effects of habitat loss and fragmentation are nonlinear, and so a more precise understanding of how altering even a small piece of viable habitat may impact the local species is rather important.

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A Appendix

In this section, we collect results related to some fundamental eigenvalue problems.

A.1 An auxiliary eigenvalue problem

Let $m \in L^\infty(\Omega)$ and consider the problem

$$\begin{cases} \Delta\phi + \lambda m\phi = 0 & \text{in } \Omega, \\ \frac{\partial\phi}{\partial\mathbf{n}} = 0 & \text{on } \partial\Omega. \end{cases} \quad (\text{A.1})$$

If there exists a value $\lambda_1(m)$ and a *positive* function ϕ_1 solving (A.1), we call $\lambda_1(m)$ the principal eigenvalue to problem (A.1). The following is a well known result and a good discussion of this problem can be found in (Cantrell and Cosner 2003). The main result is the following, with the statement taken from (Ni 2001, Chapter 4).

Proposition A.1 *Let $m \in L^\infty(\Omega)$. Problem (A.1) has a nonzero principal eigenvalue $\lambda_1(m)$ if and only if m changes sign and $\int_\Omega m \neq 0$. More precisely,*

- (i) $\int_\Omega m < 0 \Rightarrow \lambda_1(m) > 0$;
- (ii) $\int_\Omega m > 0 \Rightarrow \lambda_1(m) < 0$;
- (iii) $\int_\Omega m = 0 \Rightarrow 0$ is the only principal eigenvalue.

One can see how this relates to the statement of Proposition A.2: when the average heterogeneity is positive, $\lambda_1 < 0$ and we always have a positive eigenvalue μ_1 to problem A.2. On the other hand, when the average heterogeneity is negative, $\lambda_1 > 0$ and the sign of the eigenvalue μ_1 to problem A.2 depends on the relationship between the size of diffusion d and the size of λ_1 .

A.2 A related eigenvalue problem

Let $m \in L^\infty(\Omega)$ and consider the following eigenvalue problem:

$$\begin{cases} d\Delta\phi + m\phi + \mu\phi = 0 & \text{in } \Omega, \\ \frac{\partial\phi}{\partial\mathbf{n}} = 0 & \text{on } \partial\Omega. \end{cases} \quad (\text{A.2})$$

It seems self evident that this problem is closely related to problem A.1. We call $\mu_1(d, m)$ a principal eigenvalue for problem (A.2) whenever there exists a solution $\phi_1 \in C^+(\overline{\Omega}) \setminus \{0\}$.

It is well-known that this problem has a unique principal eigenvalue admitting the usual variational characterization:

$$\mu_1(d, m) = \inf \left\{ \int_{\Omega} [d |\nabla \phi|^2 - m \phi^2] dx : \phi \in H^1(\Omega), \int_{\Omega} \phi^2 dx = 1 \right\}. \quad (\text{A.3})$$

The following proposition highlights some of the classical properties of this eigenvalue. Recall $\lambda_1(m)$ from Subsect. A.1.

Proposition A.2 *Suppose $m \in L^\infty(\Omega)$ is not a constant function. Then the following hold.*

- (i) $\int_{\Omega} m \geq 0 \Rightarrow \mu_1(d, m) < 0$ for all $d > 0$.
- (ii) $\int_{\Omega} m < 0 \Rightarrow \begin{cases} \mu_1(d, m) < 0, & \text{if } d < \lambda_1^{-1}(m), \\ \mu_1(d, m) = 0, & \text{if } d = \lambda_1^{-1}(m), \\ \mu_1(d, m) > 0, & \text{if } d > \lambda_1^{-1}(m). \end{cases}$
- (iii) $\mu_1(d, m)$ is strictly increasing and concave with respect to $d > 0$.
- (iv) $\mu_1(d, m) < \mu_1(d, \tilde{m})$ whenever $m \not\geq \tilde{m}$.
- (v) $\mu_1(d, m)$ is continuous in m with respect to $L^\infty(\Omega)$.

Points (i)–(iv) appear in (Ni 2001), however point (v) is not explicitly discussed. Point (v) is proven in (Hess 1991) when $m_n \rightarrow m$ in $C(\overline{\Omega})$, whereas a weakened regularity case (with respect to $L^p(\Omega)$, $p > N/2$) is discussed in detail in (Daners 1997; Fleckinger and Lapidus 1986; Hess 1985), for example.

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